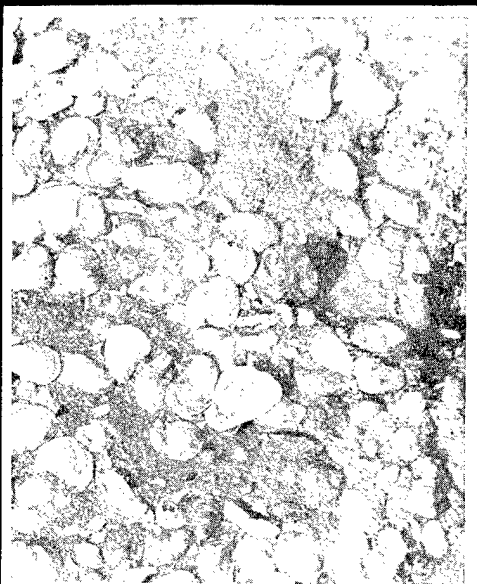
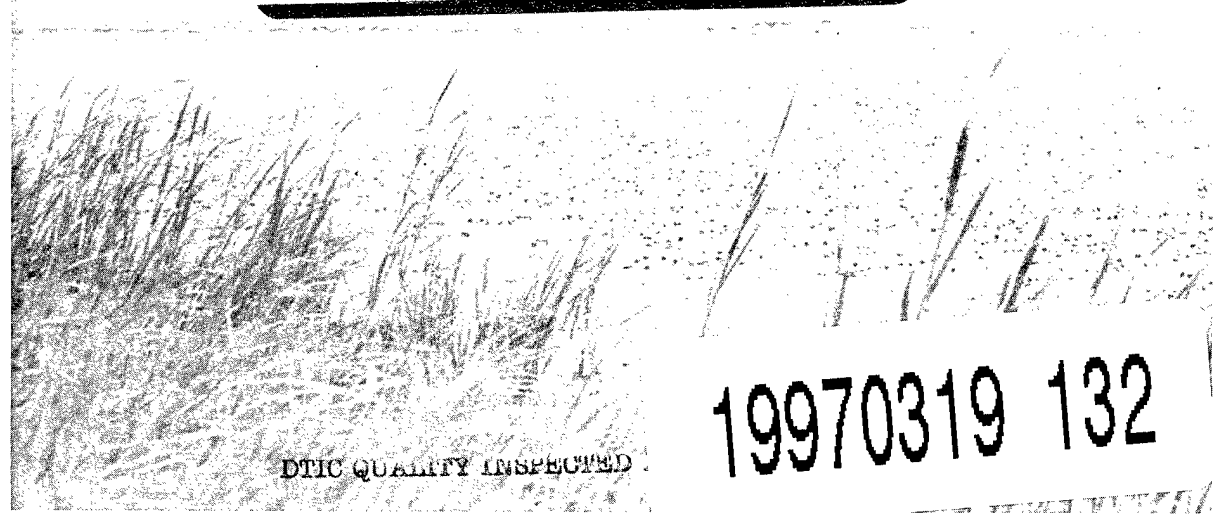


Biological Report 85(7.23)

THE ECOLOGY OF THE SOFT-BOTTOM BENTHOS OF SAN FRANCISCO BAY: A COMMUNITY PROFILE



REPRODUCTION RESTRICTED
Approved for Public Release
Distribution Unlimited



DTIC QUALITY INSPECTED

19970319 132

Fish and Wildlife Service

Geological Survey

U.S. Department of the Interior U.S. Environmental Protection Agency

Cover photographs:

Upper left: Assorted species of oyster shell accumulated on a South Bay mudflat.

Upper right: The eastern ribbed mussel, *Geukensia demissa*, an introduced species in South Bay.

Lower: Soft-bottom habitat of San Francisco Bay. Photograph courtesy of D. R. Hopkins.

Biological Report 85(1110)
September 1988

**THE ECOLOGY OF THE SOFT-BOTTOM BENTHOS
OF SAN FRANCISCO BAY: A COMMUNITY PROFILE**

by

Frederic H. Nichols
Water Resources Division
U.S. Geological Survey
345 Middlefield Road MS-496
Menlo Park, CA 94025

and

Mario M. Pamatmat
Paul F. Romberg Tiburon Center for Environmental Studies
San Francisco State University
P. O. Box 855
Tiburon, CA 94920

Project Officer

Michael Brody
National Wetlands Research Center
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

Prepared for

U.S. Department of the Interior
Fish and Wildlife Service
Research and Development
National Wetlands Research Center
Washington, DC 20240

Library of Congress Cataloging-in-Publication Data

Nichols, Frederic H. (Frederic Hone), 1937-
The ecology of the soft-bottom benthos of
San Francisco Bay

(Biological report ; 85(7.19) (Sept. 1988))

Bibliography: p.

Supt. of Docs. no.: I 49.89/2:85 (7.19)

1. Marine ecology--California--San Francisco Bay.
2. Benthos--California--San Francisco Bay. I. Pamatmat,
Mario Macalalag. II. Brody, Michael. III. National
Wetlands Research Center (U.S.) IV. Title. V. Series:
Biological report (Washington, D.C.) ; 85-7.19.

QH105.C2N53 1988 574.5'2636'091641 88-600380

This report may be cited as:

Nichols, F.H., and M.M. Pamatmat. 1988 . The ecology of the soft-bottom benthos of San Francisco Bay: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.19). 73 pp.

PREFACE

This profile, part of a series of profiles concerning coastal habitats of the United States, is a detailed examination of the soft-bottom benthos of San Francisco Bay. A U.S. Fish and Wildlife Service and California Department of Fish and Game report (1979) entitled "Protection and Restoration of San Francisco Bay Fish and Wildlife Habitat" provides clear recognition of the importance of intertidal and subtidal soft-bottom habitats and their associated organisms to the bay's birds and fishes and to the overall functioning of the estuary. The purpose of this profile is to provide a description of the structure and functioning of the benthic community in San Francisco Bay (exclusive of its tidal marshes, which are discussed by M. Josselyn [1983] in another profile). The habitats covered in this volume include all nonvegetated soft-bottom intertidal and subtidal areas of the bay between the Golden Gate and the mouths of the Sacramento and San Joaquin Rivers to the northeast, and to the southern extremity of the bay.

The profile provides a reference to the scientific information concerning the animals and plants of the bay's benthic communities, their importance to the bay ecosystem, and their value as a resource measured in human terms. Because there have been few process-oriented studies of the benthos of San Francisco Bay (e.g., field and laboratory rate-measurement experiments), the material presented herein is largely descriptive. Nonetheless, we have described the processes that interconnect the various physical, chemical, and biological components of the benthic environment, and the important couplings between this environment and the water column above, with reference to research results from other estuaries where necessary. We consider the role of

the benthic community as a food source for fish, aquatic birds, and humans; as a consumer or degrader of organic materials including wastes; as a recycler of minerals and nutrients; and as an accumulator of pollutants.

The information in the profile should be useful to environmental managers, resource planners, estuarine ecologists, marine science students, and interested laypersons who wish to learn about those components of estuarine systems that are largely unseen and unappreciated, but that play an extremely important role in the functioning of an estuary, particularly as a source of food for exploited fish stocks as well as for humans, and possibly as a biological control on eutrophication. The format, style, and level of presentation are intended to make this report adaptable to a diversity of needs, from preparation of environmental assessment reports to supplementary reading material in marine science courses.

The profile includes chapters covering geographic background (Chapter 1), biotic communities--descriptive review (Chapter 2), macrofaunal community dynamics (Chapter 3), cycling of matter in the benthos (Chapter 4), anthropogenic influences (Chapter 5), shellfisheries (Chapter 6), and managing benthic resources (Chapter 7).

The following developments have occurred since this profile was written in 1986-87: (i) There has been further resolution of the status of Macoma balthica as an introduced versus native species (Section 2.3). While it is clear that this species was originally native to San Francisco Bay, recent electrophoresis studies suggest that the present San

Francisco Bay populations are more closely related to western North Atlantic populations than to populations from Oregon and northern Europe. Thus, the San Francisco Bay and U.S. east coast Macoma populations (the former probably having been recently introduced from the latter) probably represent a separate sibling species (B.W. Meehan, Virginia Institute of Marine Science; J.T. Carlton, University of Oregon; and R. Wenne, Polish Academy of Sciences; pers. comm.) (ii) San Francisco Bay has been invaded by yet another exotic invertebrate, this time by an Asian bivalve, Potamocorbula amurensis, that was possibly transported into the bay

as larvae in ship ballast water. Increasing from one reported specimen in late 1986 to as many as 25,000/m² in summer of 1987, this clam has become the dominant macroinvertebrate throughout the northern portions of the bay and is found in South Bay sloughs as well. A shallow-dwelling suspension feeder, this clam may become a major consumer of the estuary's phytoplankton. (iii) Regarding pollution effects assessment (Section 5.3) and estuary management (Chapter 7), in April 1988, San Francisco Bay was officially designated one of the target estuaries of the U.S. Environmental Protection Agency's "National Estuary Program."

CONTENTS

| | <u>Page</u> |
|--|-------------|
| PREFACE..... | iii |
| FIGURES..... | vii |
| TABLES..... | ix |
| CONVERSION FACTORS..... | x |
| ACKNOWLEDGMENTS..... | xi |
| CHAPTER 1 - GEOGRAPHIC BACKGROUND | 1 |
| 1.1 GEOLOGIC ORIGINS | 1 |
| 1.2 PRESENT-DAY PHYSIOGRAPHY | 2 |
| 1.3 CLIMATE AND WATER PROPERTIES | 2 |
| 1.4 TIDES | 4 |
| 1.5 SEDIMENT TEXTURE AND DYNAMICS | 5 |
| CHAPTER 2- BIOTIC COMMUNITIES--DESCRIPTIVE REVIEW | 10 |
| 2.1 BACTERIA, MICROFAUNA, AND MEIOFAUNA | 10 |
| 2.2 BENTHIC MACROINVERTEBRATES | 11 |
| 2.2.1 Generalized Distributions and Relative Abundances of Common Species | 11 |
| 2.2.2 Baywide Patterns of Macroinvertebrate Biomass | 12 |
| 2.3 INTRODUCED INVERTEBRATES | 12 |
| 2.4 PREDATORS ON THE BENTHOS | 17 |
| 2.5 INVERTEBRATE FEEDING | 19 |
| 2.5.1 Feeding Modes | 19 |
| 2.5.2 Benthic Food Web | 20 |
| CHAPTER 3 - MACROFAUNAL COMMUNITY DYNAMICS | 21 |
| 3.1 SEASONAL PATTERNS IN THE BENTHIC COMMUNITY | 21 |
| 3.1.1 Abundance Changes | 21 |
| 3.1.2 Seasonal Growth | 23 |
| 3.1.3 Seasonal Predation | 24 |
| 3.2 APERIODIC PATTERNS OF ABUNDANCE | 24 |
| 3.2.1 Effects of Environmental Perturbations | 24 |
| 3.2.2 Importance of Species Interactions | 26 |
| 3.3 LONG-TERM TRENDS | 26 |
| CHAPTER 4 - CYCLING OF MATTER IN THE BENTHOS | 28 |
| 4.1 INTRODUCTION | 28 |
| 4.2 SOURCES OF ORGANIC MATTER | 28 |
| 4.2.1 Vascular Plants | 28 |
| 4.2.2 Benthic Macroalgae | 29 |
| 4.2.3 Phytoplankton | 29 |
| 4.2.4 Benthic Bacteria and Microalgae | 30 |
| 4.2.5 Microalgal Production | 31 |
| 4.2.6 Other Sources of Organic Matter to the Benthos | 32 |
| 4.3 RATE OF ORGANIC MATTER SUPPLY | 32 |
| 4.4 FATE OF ORGANIC MATTER IN SEDIMENTS | 33 |
| 4.5 SEDIMENT OXYGEN CONSUMPTION | 34 |

| | <u>Page</u> |
|---|-------------|
| 4.6 BENTHIC NUTRIENT REGENERATION IN SAN FRANCISCO BAY | 35 |
| 4.7 MODELS OF ORGANIC MATTER BUDGETS OF ESTUARINE BENTHOS..... | 36 |
| CHAPTER 5 - ANTHROPOGENIC INFLUENCES | 38 |
| 5.1 EARLY PHYSICAL AND BIOLOGICAL CHANGES | 39 |
| 5.2 INTERFERENCE WITH THE NATURAL HYDROLOGIC CYCLE | 39 |
| 5.3 EFFECTS OF POLLUTION | 41 |
| 5.3.1 Methods of Evaluation | 42 |
| 5.3.2 Sewage-Induced Nutrient Enrichment | 46 |
| 5.3.3 Effect of Pollution on Benthic Community Metabolism | 46 |
| 5.4 SEDIMENT BUDGET AND DREDGING | 47 |
| 5.4.1 Estimates of Sediment Budget | 47 |
| 5.4.2 Effects of Dredging on the Benthos..... | 47 |
| 5.4.3 Effects of Contaminated Dredged Sediments on Organisms | 48 |
| 5.4.4 Effect of Channel Dredging on Saltwater Intrusion | 49 |
| CHAPTER 6 - SHELLFISHERIES | 50 |
| 6.1 EARLY HISTORY OF BAY SHELLFISHERIES | 50 |
| 6.1.1 Oysters | 50 |
| 6.1.2 Clams and Mussels | 52 |
| 6.1.3 Crabs | 52 |
| 6.1.4 Shrimp | 53 |
| 6.2 PRESENT STATUS OF BAY SHELLFISHERIES | 53 |
| 6.2.1 Sport Harvesting of Mollusks | 53 |
| 6.2.2 Commercial Harvesting of Crustaceans | 53 |
| 6.3 THE FUTURE OF BAY MOLLUSK FISHERIES | 54 |
| 6.3.1 Oysters | 54 |
| 6.3.2 Clams | 54 |
| 6.3.3 The Threat of Pollution | 54 |
| CHAPTER 7 - MANAGING BENTHIC RESOURCES | 55 |
| 7.1 INTRODUCTION | 55 |
| 7.2 PUBLIC PERCEPTIONS, USES, AND CONCERNS | 55 |
| 7.3 SCIENTIFIC BASIS FOR MANAGEMENT | 56 |
| 7.3.1 Present Knowledge | 56 |
| 7.3.2 Hindrances to Increased Understanding | 57 |
| 7.4 NEEDS FOR RESEARCH AND MANAGEMENT | 58 |
| REFERENCES..... | 61 |

FIGURES

| <u>Number</u> | | <u>Page</u> |
|---------------|--|-------------|
| 1 | Drainage basin of the Sacramento-San Joaquin Rivers | 1 |
| 2 | The Pacific coast of the United States | 1 |
| 3 | Past shorelines of San Francisco Bay | 3 |
| 4 | The San Francisco Bay Estuary | 4 |
| 5 | Bathymetry of San Francisco Bay | 5 |
| 6 | Horizontal and vertical distribution of salinity | 6 |
| 7 | Horizontal and vertical distribution of turbidity | 7 |
| 8 | A mudflat of South Bay | 7 |
| 9 | Generalized distribution of surface sediment texture | 8 |
| 10 | Percentage of mud collected in the shallows of four embayments | 9 |
| 11 | Accumulated oyster shells of assorted species on a mudflat | 13 |
| 12 | Cumulative number of introduced mollusks by date of discovery | 14 |
| 13 | Distribution and abundance of an introduced amphipod | 15 |
| 14 | The introduced eastern ribbed mussel at the edge of a cordgrass marsh | 16 |
| 15 | Eroding edge of a San Francisco Bay marsh, perforated by burrows of an introduced isopod | 16 |
| 16 | An unusually high concentration of the introduced mudsnail | 16 |
| 17 | Proportions of introduced and native species relative to total biomass of mollusks | 16 |
| 18 | The salt-panne habitat of the native hornsnail | 17 |
| 19 | Feeding depressions, probably made by the bat ray | 17 |
| 20 | Clam feeding traces, with the mudsnail for scale | 20 |
| 21 | Abundance of the macrofauna collected in core samples on an intertidal mudflat | 22 |
| 22 | Abundance of three numerically dominant mudflat species over a 10-year period | 22 |
| 23 | Average length of individuals in two age classes of a native clam | 23 |
| 24 | Salinity, mean number of macrofauna species, and mean number of individuals at a shallow site in Suisun Bay | 25 |
| 25 | Average abundance of numerically abundant species at two sites in Suisun Bay | 25 |
| 26 | Freshwater flow into San Francisco Bay and abundance of two species at a mudflat study site | 26 |
| 27 | Contours of near-surface phytoplankton biomass (measured as chlorophyll) in San Francisco Bay | 30 |
| 28 | Average chlorophyll concentration in surface sediments at sites less than 5 m water depth | 31 |
| 29 | Daily maximum ebb tidal velocity, average monthly wind velocity, and average monthly irradiance at low tide | 31 |

| <u>Number</u> | | <u>Page</u> |
|---------------|--|-------------|
| 30 | Relations among aerobic processes and anaerobic processes in sediments | 33 |
| 31 | Distribution of Indian shell middens at about 1900 | 38 |
| 32 | Relation between the winter maximum concentration of silver in clams and the rate of freshwater inflow | 41 |
| 33 | Distribution and abundance of a polychaete species from results of many quantitative surveys | 43 |
| 34 | Concentrations of silver in a clam from a South Bay study site | 44 |
| 35 | Relation between the depth of the river-estuary channel and the extent of landward intrusion of salt | 49 |
| 36 | Location of former oyster beds | 51 |
| 37 | Breakwater provides habitat and refuge for two introduced clam species | 53 |
| 38 | A typical bay view | 56 |

TABLES

| <u>Number</u> | <u>Page</u> |
|--|-------------|
| 1 Wet weight and percent of total sample wet weight for different faunal groups in each region of the bay | 12 |
| 2 Percent composition of food items occurring in the gizzard of shorebirds collected at Palo Alto | 18 |
| 3 Reported feeding modes of common soft-bottom macroinvertebrates found in San Francisco Bay | 19 |
| 4 Rates of benthic oxygen uptake and carbon dioxide production in South Bay | 34 |

CONVERSION TABLE

Metric to U.S. Customary

| <i>Multiply</i> | <i>By</i> | <i>To Obtain</i> |
|--------------------------------------|--------------|-----------------------|
| millimeters (mm) | 0.03937 | inches |
| centimeters (cm) | 0.3937 | inches |
| meters (m) | 3.281 | feet |
| meters (m) | 0.5468 | fathoms |
| kilometers (km) | 0.6214 | statute miles |
| kilometers (km) | 0.5396 | nautical miles |
| square meters (m ²) | 10.76 | square feet |
| square kilometers (km ²) | 0.3861 | square miles |
| hectares (ha) | 2.471 | acres |
| liters (l) | 0.2642 | gallons |
| cubic meters (m ³) | 35.31 | cubic feet |
| cubic meters (m ³) | 0.0008110 | acre-feet |
| milligrams (mg) | 0.00003527 | ounces |
| grams (g) | 0.03527 | ounces |
| kilograms (kg) | 2.205 | pounds |
| metric tons (t) | 2205.0 | pounds |
| metric tons (t) | 1.102 | short tons |
| kilocalories (kcal) | 3.968 | British thermal units |
| Celsius degrees (°C) | 1.8(°C) + 32 | Fahrenheit degrees |

U.S. Customary to Metric

| | | |
|---------------------------------|------------------|-------------------|
| inches | 25.40 | millimeters |
| inches | 2.54 | centimeters |
| feet (ft) | 0.3048 | meters |
| fathoms | 1.829 | meters |
| statute miles (mi) | 1.609 | kilometers |
| nautical miles (nmi) | 1.852 | kilometers |
| square feet (ft ²) | 0.0929 | square meters |
| square miles (mi ²) | 2.590 | square kilometers |
| acres | 0.4047 | hectares |
| gallons (gal) | 3.785 | liters |
| cubic feet (ft ³) | 0.02831 | cubic meters |
| acre-feet | 1233.0 | cubic meters |
| ounces (oz) | 28350.0 | milligrams |
| ounces (oz) | 28.35 | grams |
| pounds (lb) | 0.4536 | kilograms |
| pounds (lb) | 0.00045 | metric tons |
| short tons (ton) | 0.9072 | metric tons |
| British thermal units (Btu) | 0.2520 | kilocalories |
| Fahrenheit degrees (°F) | 0.5556 (°F - 32) | Celsius degrees |

ACKNOWLEDGMENTS

Many people have helped us during the preparation of this profile. J.K. Thompson (U.S. Geological Survey), a long-time colleague of the first author, has provided immeasurable assistance both in gathering and interpreting the San Francisco Bay benthos data that comprise a large part of the material presented herein. R.N. Tasto, T.O. Moore (California Department of Fish & Game) and D.W. Price (California Department of Health Services) provided much useful material and comments concerning bay shellfish. S. Wyllie Echeverria (California State University, San Francisco) brought us up to date concerning ongoing studies of eelgrass beds. J.E. Cloern, S.N. Luoma, and D.S. McCulloch (U.S. Geological Survey) provided comments on various individual chapters. D.R. Hopkins (U.S. Geological Survey) reviewed the profile for typographical errors and provided

photographs (as indicated in captions; all other photographs taken by the first author) including that on the cover. J. Dileo-Stevens (U.S. Geological Survey) drafted all of the illustrations. J.T. Carlton (University of Oregon), E.B. Lyke (California State University, Hayward), M.N. Josselyn (California State University, San Francisco), M.S. Race (University of California, Berkeley), J.K. Thompson (U.S. Geological Survey), and an anonymous reviewer provided detailed and immensely helpful reviews of the entire manuscript. Finally, M.S. Brody, as Project Officer (U.S. Fish and Wildlife Service), was extremely patient and helpful as we prepared the profile. To all of these people, we offer our thanks.

Funding for this report was provided by the U.S. Environmental Protection Agency, Region 9 office.

CHAPTER 1. GEOGRAPHIC BACKGROUND

1.1 GEOLOGIC ORIGINS

San Francisco Bay is located at the mouth of the Sacramento-San Joaquin River system which carries runoff from tributary rivers and streams draining about 40% (153,000 km²) of California's surface area (Figure 1). The surface area of the estuary (1,240 km²) makes it the largest coastal bay on the Pacific coast of the United States (Figure 2) and one of North America's largest estuaries.

The topography of the San Francisco Bay region results from recent deformation

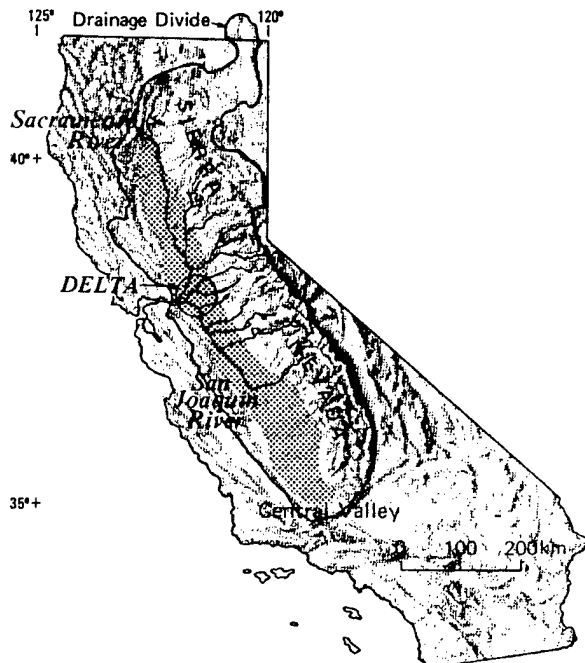


Figure 1. California and the drainage basin of the Sacramento-San Joaquin Rivers; Central Valley indicated by stippling (adapted from Conomos et al. 1985).

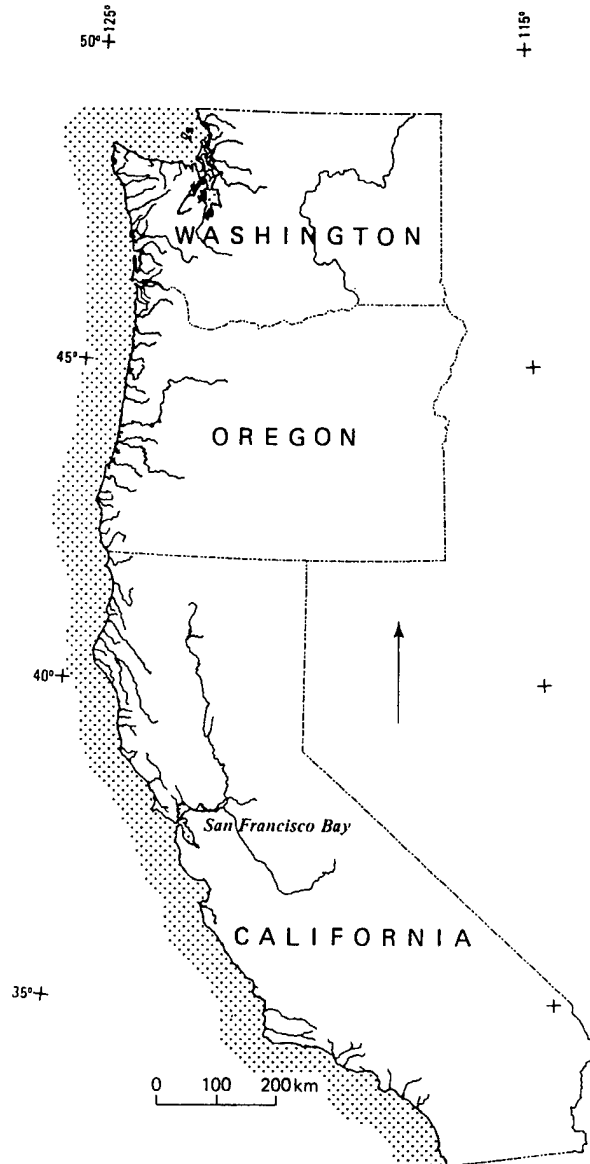


Figure 2. The Pacific coast of the United States, illustrating the geographic separation of large west coast estuaries and the relatively larger size of the San Francisco Bay Estuary and its drainage system.

of an older, tectonically active continental margin. The coastal region of western North America is composed of large blocks of discrete geologic terranes that were carried hundreds of kilometers northward and accreted to the North American continent (Howell 1985). Between 3 and 5 million years ago, stresses exerted across the continental margin uplifted the present Coast Ranges. The long process of mountain building left only a narrow continental shelf and little coastal plain. Most rivers flowing through the coastal mountains drain relatively small, mostly arid areas. As a result, most estuaries along the west coast (Figure 2) are small.

Local subsidence created the bedrock trough in which San Francisco Bay lies (Atwater 1979). Sea-level fluctuations during the past few million years have created (and subsequently destroyed) estuarine embayments in the trough at the site of the present San Francisco Bay (Atwater 1979). Core samples taken within bay sediments suggest that there have been at least three cycles of submergence and emergence of the bay region, associated with the major periods of glaciation, in the million years before the formation of the present estuary (Atwater 1979). After the end of the last glacial period, about 15,000 to 18,000 years ago, the sea began its most recent rise and entered the bay about 10,000 years ago. By 5,000 years ago, the area of the estuary was nearly what it is today (Figure 3). As polar icecap melting slowed during recent millennia, submergence of the bay slowed, and much of the relative change in sea level in the bay region since results from crustal subsidence (Atwater et al. 1977).

1.2 PRESENT-DAY PHYSIOGRAPHY

Freshwater flows from the rivers and streams of the Sacramento and San Joaquin River system meet in a complex of islands and channels (the Delta), then empty into the northeastern end of San Francisco Bay (Figure 1). The total flow into the estuary from the Delta represents about 90% of the annual river inflow to San Francisco Bay. All other rivers and streams entering the bay are comparatively small, and most of these are intermittent with little or no flow during the summer months (Conomos et al. 1985).

San Francisco Bay comprises separate embayments: a deeper central region near the City of San Francisco (Central Bay), and shallower regions (Suisun, San Pablo, and South Bays; Figure 4) that are characterized by broad shallows incised by narrow channels (Figure 5) whose depths are maintained by river and tidal scouring. The average depth of the bay is about 6 m at mean lower low water while median depth is about 2 m (Conomos et al. 1985). The perimeter of the bay, which once comprised large fresh- and saltwater marshes, is now largely diked (Section 5.1), although salt evaporating ponds and seasonal wetlands (some of them used for farming during the dry season) continue to provide wildlife habitat (Josselyn 1983). Undiked marshes remain only at isolated locations.

1.3 CLIMATE AND WATER PROPERTIES

California's climate consists of a mild, wet winter season (November-April) and a dry summer season (May-October). As a result, river inflow is high during the midwinter months (1,000 to 10,000 m³/s) and low (100-400 m³/s) during summer and fall (Conomos et al. 1985). The strongly seasonal pattern of rainfall and runoff imparts a similarly strong influence on the physical and chemical properties of the estuary, seen most readily as marked season-to-season differences in the salinity of bay waters (Figure 6). During a normal winter, low-salinity (brackish) water (less than 2 ppt) is found at the eastern end of San Pablo Bay, and salinity in South Bay can fall below 15 ppt. During summer, brackish water is found at the eastern end of Suisun Bay (and occasionally farther upstream), while the water in South Bay can be as saline as the adjacent ocean. Water temperature varies only about 10°C through the year (roughly from 10 to 20°C).

River-induced seasonal variations in the salinity regime greatly influence the dynamics of biological populations (Cloern and Nichols 1985). During high-winter river inflows and lowered salinity, pelagic species populations (phytoplankton, zooplankton, fish) in the northern reaches of the bay can be displaced downstream by both physical advection and voluntary migration. This river inflow-induced movement also affects some benthic species populations (Chapter 3).

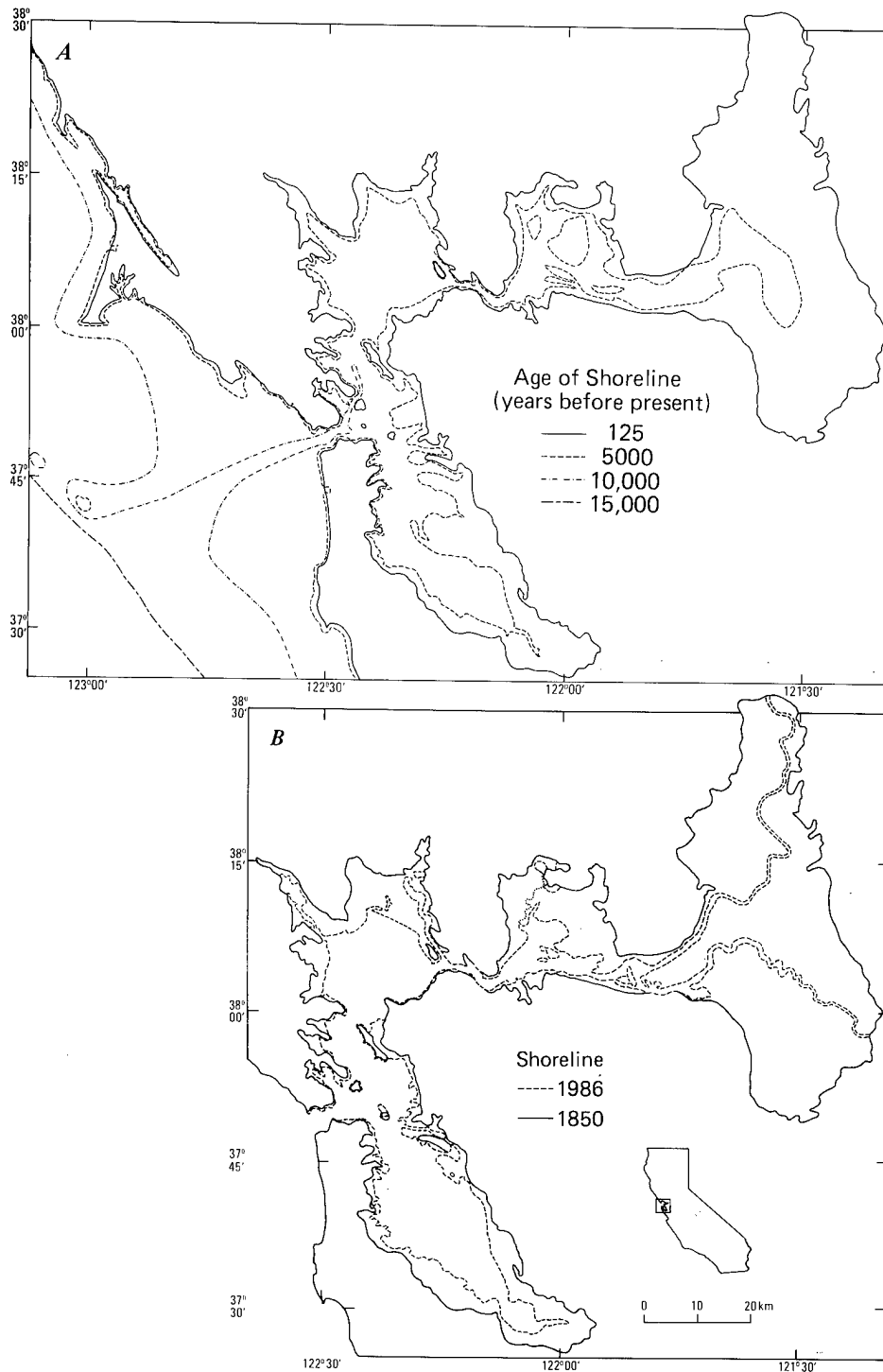


Figure 3. Past shorelines of San Francisco Bay. (A) The advancement of sea level during the past 15,000 years (adapted from Atwater 1979); (B) the approximate position of the shoreline of the bay (landward edge of undiked tidal marshes) in 1850 and at present (adapted from Atwater et al. 1979).

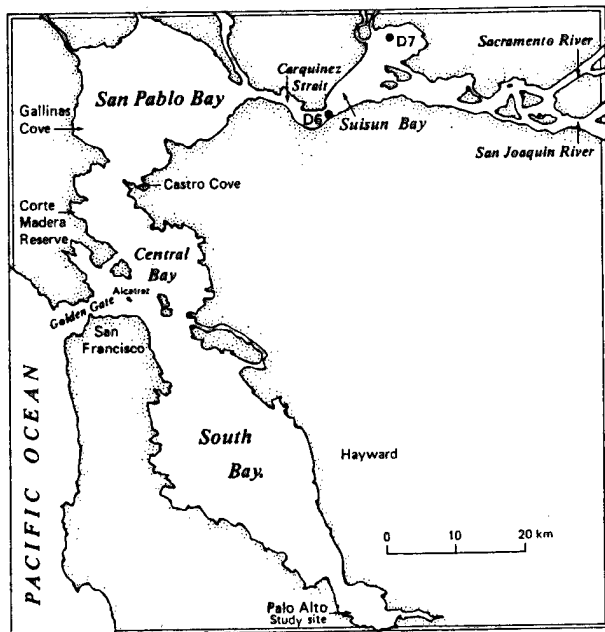


Figure 4. The San Francisco Bay Estuary. Sites D6 and D7 in Suisun Bay are California Department of Water Resources sampling locations for data shown in Figures 24 and 25.

River inflow is the major source of the approximately 4.3×10^6 tons of sediment that enter the bay each year from the rivers, 80% of it from the Sacramento-San Joaquin River drainage basin (Porterfield et al. 1961, Conomos et al. 1985). Most of the total sediment input occurs during winter, greatly increasing the turbidity of the water (Figure 7) as well as sedimentation throughout the estuary.

Strong seasonal winds are important in controlling water circulation and mixing (Conomos et al. 1985). Prevailing west and northwest winds, reinforced by solar heating of air masses in inland California, are strongest during the summer. These winds generate complex bay-wide water circulation patterns that are superimposed on tide- and river-induced circulation (Walters et al. 1985). The complex wind-induced circulation patterns have important implications for all physical and biological processes in the estuary (Cloern and Nichols 1985). Some of the effects of circulation patterns on the benthos are discussed in Chapter 4. Winds are also a major factor in controlling oxygen concentrations in the estuary.

Hartman and Hammond (1985) have shown that wind stress on the water surface is the dominant factor maintaining water column oxygen at or near atmospheric equilibrium concentrations at all depths throughout the estuary. As a result, the benthos of San Francisco, unlike that of other estuaries (e.g., in the Chesapeake Bay estuarine complex; Officer et al. 1984), is not limited by low oxygen. This was not the case several decades ago when the disposal of poorly treated wastes caused severe depletion of water column oxygen, particularly in South Bay in summer (Section 5.1). Wind mixing was apparently not sufficient to counteract the effect of waste-related oxygen demand before the construction of modern waste-treatment facilities.

1.4 TIDES

Tides influence the dynamics of plant and animal species populations. In particular, they affect biological productivity in intertidal and subtidal sediments by moving and mixing water masses (and associated organisms) and by varying the height of the water column above the bottom over a variety of time scales from hours to seasons. Tides also help to disperse larvae, juveniles, and adults of benthic species (Section 3.1.1).

The tidal range (maximum difference between high water and low water elevations) is greatest (2.6 m) at the extremity of South Bay, decreasing to 1.7 m at the Golden Gate (the bay's narrow connection to the ocean), 1.3 m at Suisun Bay, and to progressively narrower ranges farther upstream. Such tidal ranges, relative to the average bay depth of 6 m, contribute to a tidal prism (the volume of water between low and high tide levels that passes in and out of the bay during each tidal cycle) that is about 24% of the bay's total volume. The large, rapid exchange of water with the ocean produces strong tidal currents throughout the bay, particularly at physiographic constrictions such as Carquinez Strait and the Golden Gate (Figure 4). Current velocities at the Golden Gate can reach 280 cm/s.

The tides are of the mixed semidiurnal variety, with two lows and two highs

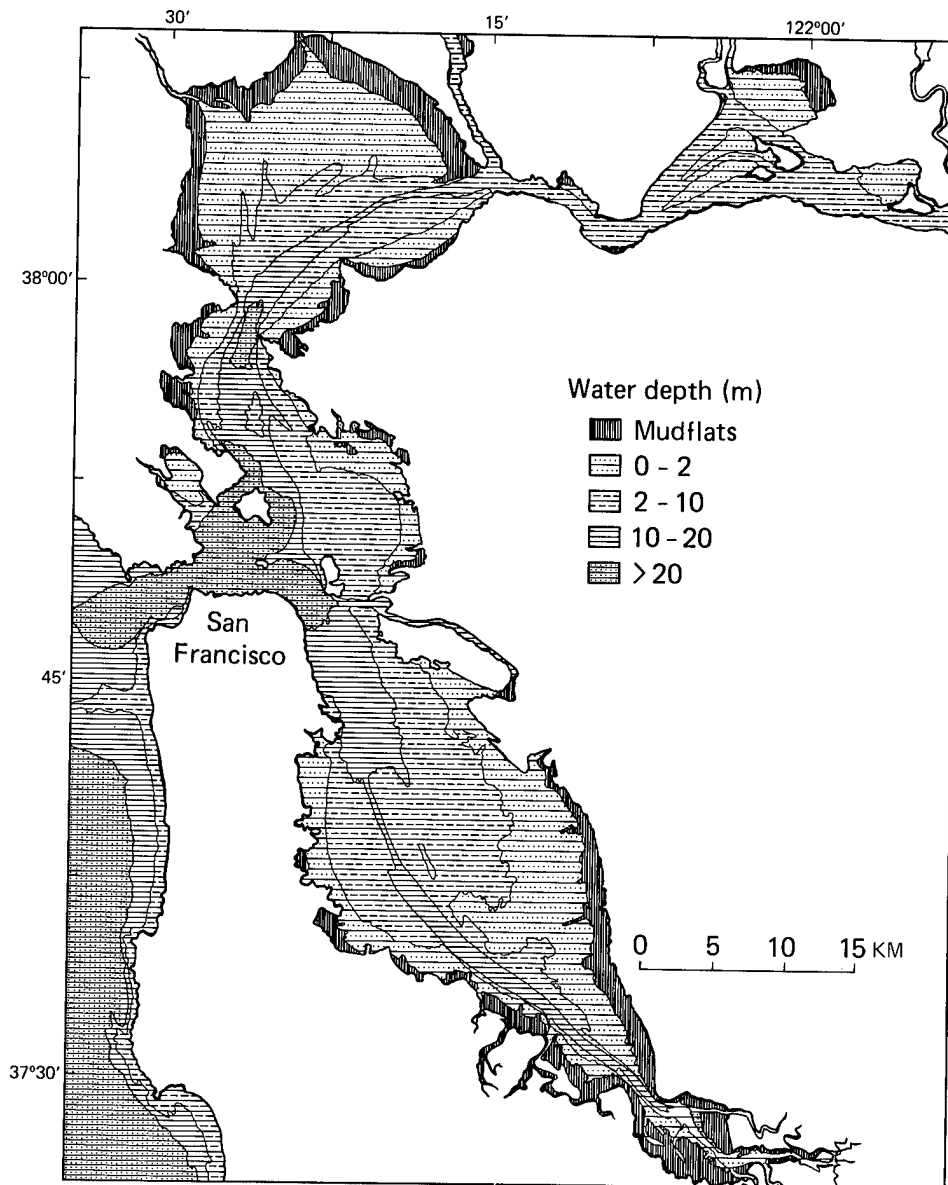


Figure 5. Bathymetry of San Francisco Bay (adapted from Nichols and Thompson 1985a).

during each 24.84 hours. Any two successive highs or successive lows are usually very different in height. In any month the intertidal zone is exposed day and night during both neap and spring tides. Nonetheless, there is a seasonality in the occurrence of extreme low and high water: the greatest tidal exposure of the mudflats occurs at night in the winter months and during the day in spring and summer months. This phenomenon accentuates the spring growth of benthic plants

(Section 4.2.4) which, in turn, contributes to highly seasonal growth of benthic herbivores (Section 3.1.2).

1.5 SEDIMENT TEXTURE AND DYNAMICS

Nearly half of the surface area of San Francisco Bay at high tide is covered by water less than 2 m deep, and more than 15% is above the level of mean lower low

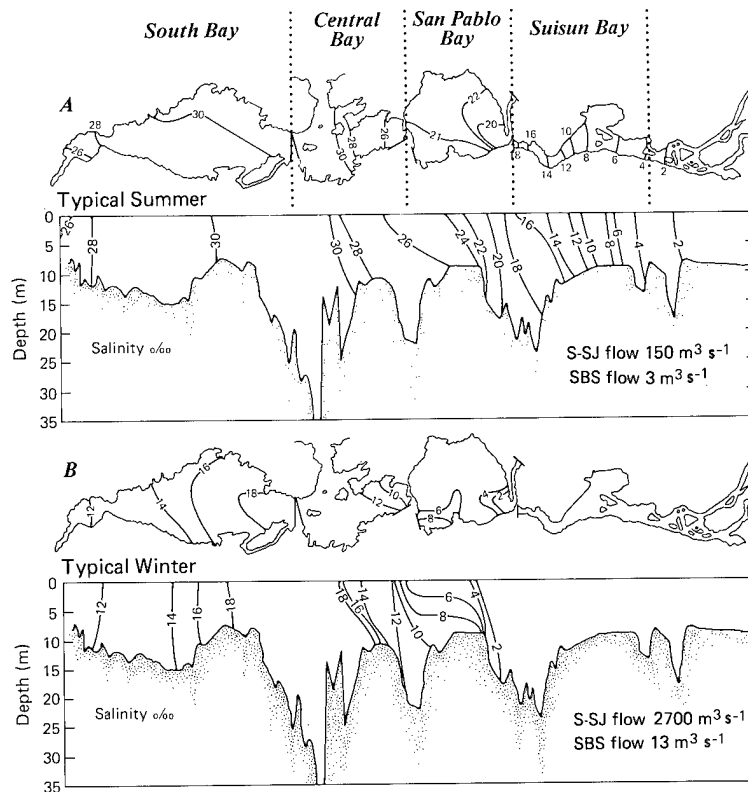


Figure 6. Horizontal and vertical distribution of salinity, uncorrected for tidal variations, under typical summer (A) and winter (B) flows for the Sacramento-San Joaquin River system (S-SJ) and South Bay streams (SBS); plan view distorted for ease of display (adapted from Conomos et al. 1985).

water. These broad areas with little vertical relief (Figure 8) are covered with soft mud (generally more than 80% silt + clay). Mud is found at all depths in the southern end of the bay, although the mud of large areas of the eastern shallows of South Bay is mixed with shell fragments--remnants of once-thriving beds of native and introduced oysters (Chapter 6). Strong tidal currents and river-induced gravitational currents, particularly during winter, are focused in the deep areas of Central Bay, in the narrow straits separating the major embayments, and in the narrow midbay channels (Figure 5). This focusing of currents contributes to well-winnowed, coarse channel-bottom sediments in the central and northern embayments (Figure 9). Conversely, current velocities are lower over the lateral shoals in each embayment, permitting the deposition of fine sediments supplied by

the rivers and resuspended by wind waves and tidal currents.

The bottom of Central Bay is covered by sand waves up to 8 m high that move with the strong ebb and flood tidal flow through the Golden Gate (Rubin and McCulloch 1979). Only along the shallow eastern shoreline of this area does mud again predominate (Figure 9). Surface sediment texture varies markedly with time as a result of seasonal variations in river inflow, tides, and winds (Thompson et al. 1981; Nichols and Thompson 1985b). Much of the fine-grained river-borne sediment that is transported down river during the high-flow periods of winter and early spring bypasses Suisun Bay and accumulates in San Pablo Bay (Klingeman and Kaufman 1963, 1965; Conomos and Peterson 1977). In the process, Suisun Bay fine sediment is winnowed during the high-flow season,

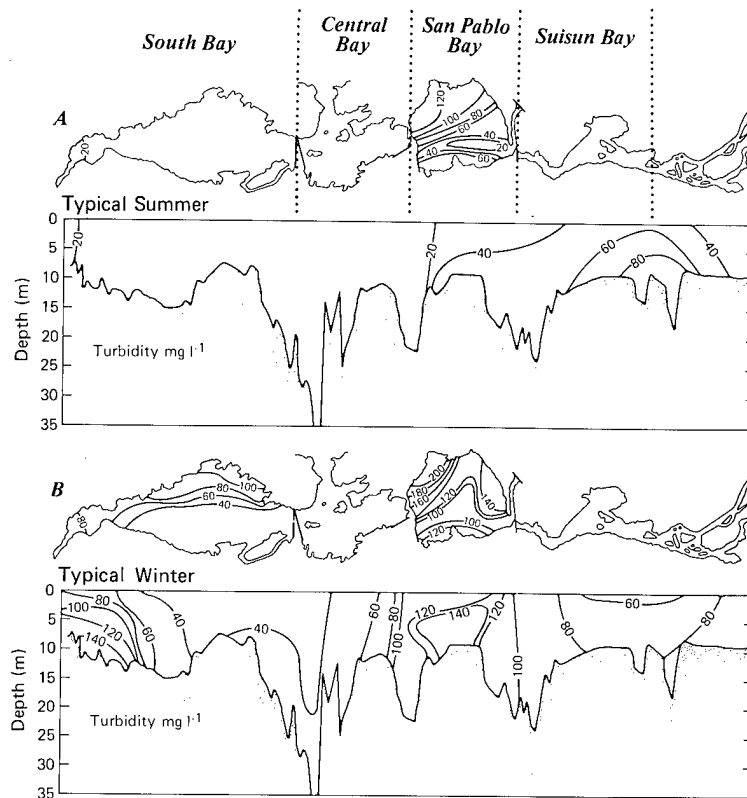


Figure 7. Horizontal and vertical distribution of turbidity, uncorrected for tidal variations, under typical summer (A) and winter (B) conditions; plan view distorted for ease of display (adapted from Conomos et al. 1985).



Figure 8. A mudflat of South Bay.

leaving relatively more coarse sediment (Figure 10). During summer and autumn the pattern is reversed: fine sediment is resuspended and transported away from San Pablo Bay at the same time that it is being deposited in Suisun Bay. In South Bay, sediments may locally accumulate on intertidal mudflats during autumn and winter, but these deposits are usually removed during the following spring and summer (Figure 10), a result of increased wind- and tide-induced current scour (Nichols and Thompson 1985b).

Repeated deposition and resuspension of the same sediments are predominant characteristics of San Francisco Bay. Fuller (1982) concluded from a comparison of resuspension and accumulation rates

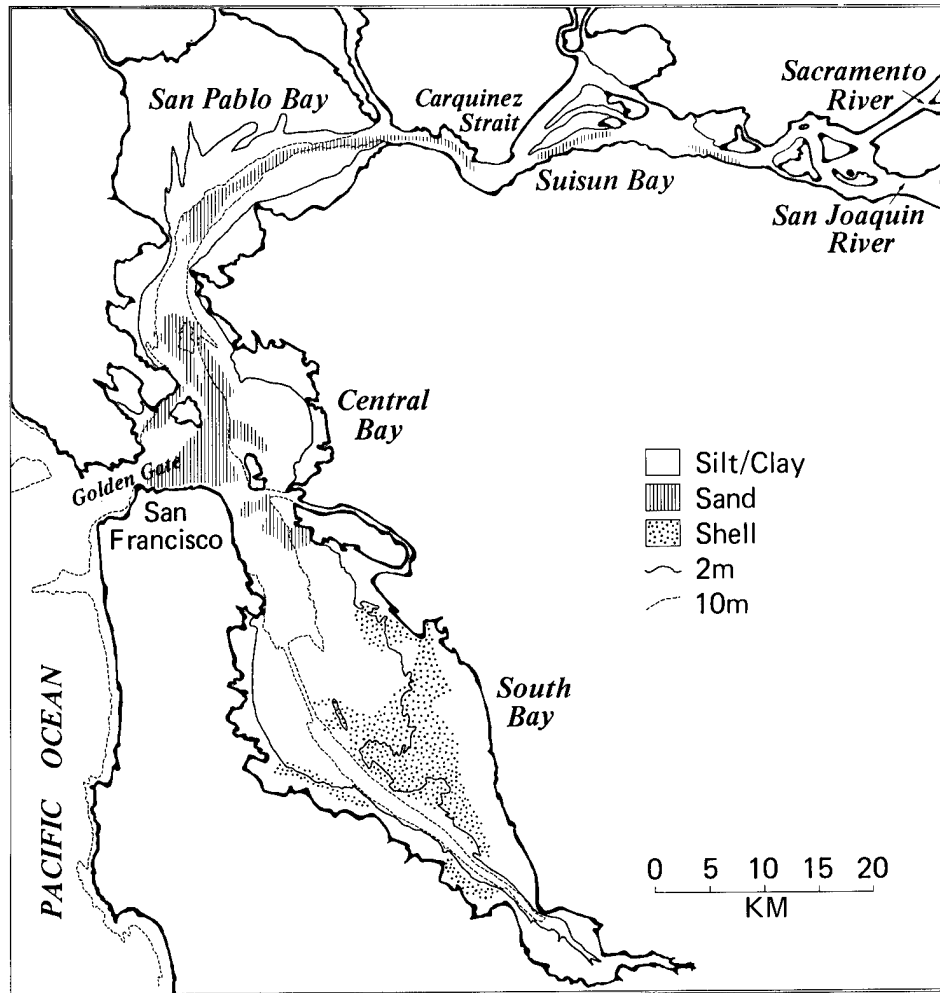


Figure 9. Generalized distribution of surface sediment texture in San Francisco Bay (from Nichols and Thompson 1985b).

that sediments in deep areas of South Bay are resuspended at least two to five times before final burial. Apparently superimposed on typical seasonal cycles of deposition and resuspension are intense periods of erosion or deposition that can rapidly change the sediment surface (Section 3.2.1; Nichols and Thompson 1985a).

Surface sediments are well oxidized throughout the year in San Francisco Bay, largely because the water column above remains well oxygenated. Occasionally, localized accumulations of decaying macroalgal species following unusual summer blooms (Horne and Nonomura 1976; Josselyn and West 1985) have resulted in anoxia at the sediment surface (Section 3.2.1).

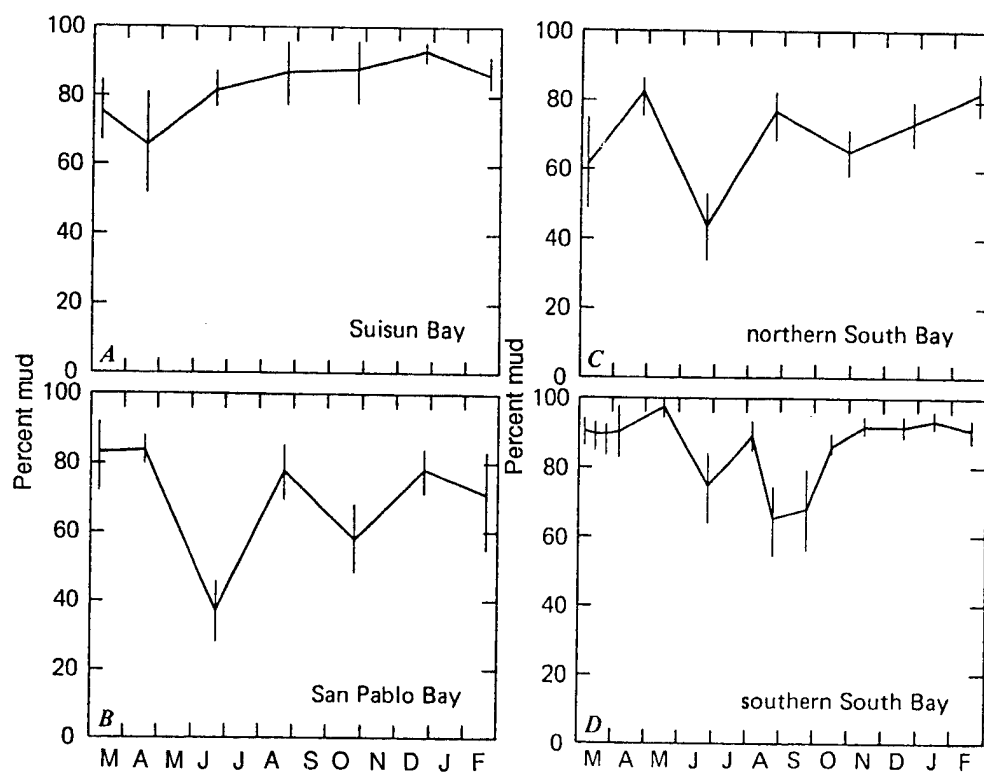


Figure 10. Percentage of mud (silt + clay) collected in the shallows (less than 5-m deep) during 1980-81 in four embayments of San Francisco Bay; average of 4-6 stations in each embayment (from Nichols and Thompson 1985b).

CHAPTER 2. BIOTIC COMMUNITIES--DESCRIPTIVE REVIEW

The benthos of the estuary encompasses a wide range of taxonomic and functional entities, from bacteria to large crabs. This profile focuses, however, only on infaunal invertebrates, the smaller, relatively sessile animals living on or in surface sediments that can be collected in core or grab samples. In this chapter we consider the distribution and abundance of the major taxonomic categories of invertebrates primarily by size groupings, although in many cases these are functional groupings as well. In the following chapter, we consider the population dynamics within macrobenthic species and species groups, as well as the interactions among them.

2.1 BACTERIA, MICROFAUNA, AND MEIOFAUNA

The smaller organisms of aquatic benthic communities include the microfauna (unicellular organisms such as flagellates and ciliates that are seen only under high magnification) and meiofauna (small metazoans that are mostly visible with the unaided eye but require low magnification for identification and counting, along with some large unicellular forms). The meiofauna, generally in the size range of 0.1 to 0.5 mm, is a diverse group that includes permanent meiofauna (nematodes, ostracods, kinorhynchids, harpacticoid copepods, foraminiferans) and temporary meiofauna (the larvae and young of the macrofauna). The largest animals, the macrofauna, are those organisms that are retained on a 0.5-mm sieve.

The relative densities and biomass of bacteria, microfauna, meiofauna, and macrofauna vary among the many benthic systems studied (Gerlach et al. 1985). What is known from studies worldwide, however, suggests that small organisms can be important. For example, Fenchel (1969) showed that while macrofauna may be

dominant in biomass, the smaller ciliates may be dominant in terms of total metabolism.

The role of meiofauna in the benthos is still being clarified. Considerable research on meiofauna in other estuaries has demonstrated the importance of its role in benthic food webs (Coull 1973; Coull and Bell 1979; Reise 1979; Heip 1980; Bouwman et al. 1984). In the Dutch Wadden Sea, for example, the meiofauna may be more important than the macrofauna in the trophic chain leading to demersal fish production (Kuipers et al. 1981).

Quantitative knowledge of bacteria, microfauna, and meiofauna in San Francisco Bay is, however, nearly nonexistent. Some bacterial processes in San Francisco Bay sediments have been studied (Sections 4.2 and 4.4). But, other than several studies of recent foraminiferan distributions in San Francisco Bay (Arnal et al. 1980, and the papers cited therein), no literature exists on the bay meiofauna. Their small size and the absence of local specialists on this group (other than for the foraminifera) have contributed to the paucity of published studies. An unpublished study of the abundance of meiofauna in oxygenated surface sediments of the eastern shore of South Bay near Hayward showed the presence of more than 2.5×10^6 nematode worms per square meter, more than 5×10^5 harpacticoid copepods per square meter, and fewer amphipods, polychaetes, ostracods, and foraminiferans (E.B. Lyke, California State University, Hayward; pers. comm.). Other unpublished observations of meiofaunal distributions at two locations on the western shore (Corte Madera and Palo Alto; Figure 4) showed that ostracods and nematodes predominate in muddy intertidal sediments, while harpacticoids are much less numerous (M.M. Pamatmat, unpubl.).

2.2 BENTHIC MACROINVERTEBRATES

2.2.1 Generalized Distributions and Relative Abundances of Common Species

The distribution of species in the oft-studied soft-bottom macrobenthic invertebrate community of San Francisco Bay (organisms retained on 0.5 or 1.0-mm screens) appears to be most strongly influenced by temporal variations in salinity (Nichols 1979; Nichols and Thompson 1985b). Away from the marine environment of Central Bay, the benthos is characterized by low diversity and dominated numerically by a few species (common to many U.S. estuaries) that are tolerant of wide salinity variations (Nichols and Thompson 1985a).

Suisun Bay is a brackish-water embayment characterized by islands and shallow sub-bays intersected by tide- and river-scoured channels. It is inhabited by fewer than 10 permanent macrobenthic species because the region is inundated each winter by freshwater. Species that can survive there include the mollusks Macoma balthica, Mya arenaria (and occasionally the freshwater species Corbicula fluminea when river inflow is unusually high); the amphipods Corophium stimpsoni and C. spinicorne; and the annelids Nereis succinea and Limnodrilus hoffmeisteri (Filice 1958; Aldrich 1961; Painter 1966; California Department of Water Resources 1986). Occasionally, during prolonged periods of low river flow and increased salinity, the polychaete Streblospio benedicti and the amphipod Ampelisca abdita (identified until recently as Ampelisca milleri, and in some reports during the 1960's as Photis californica; Carlton 1979a,b) migrate upstream to Suisun Bay (Nichols 1985b). These latter two species are normally restricted to the parts of the bay west of Carquinez Strait because of their intolerance of freshwater.

West of Carquinez Strait, where salinity seldom falls below 5 ppt, diversity increases (Filice 1958; Nichols 1979). The macrobenthic community of the broad, shallow subtidal expanses of San Pablo Bay comprises, in addition to Macoma balthica and Mya arenaria, the mollusks Gemma gemma, Musculista senhousia, Tapes

philippinarum (= Tapes japonica), and Ilyanassa obsoleta; the amphipods Ampelisca abdita, Grandidierella japonica, and Corophium spp.; the polychaetes Streblospio benedicti, Heteromastus filiformis, Glycinde sp., and several species of Polydora including P. ligni; and several oligochaetes (Filice 1958; Hopkins 1986; F.H. Nichols and J.K. Thompson, U.S. Geological Survey, unpubl.). Some of these species are "euryhaline opportunists" (Grassle and Grassle 1974; Boesch 1977) that are common in many U.S. estuaries. Macoma balthica predominates in both abundance and biomass in the macrobenthic community of the broad shallow intertidal reaches of northern San Pablo Bay. The abundance of other species that are common subtidally may be limited in shallow areas by reduced salinities and heavy siltation during winter and windwave scouring in summer (Hopkins 1987).

The estuarine community typical of San Pablo Bay grades into a marine community in the deeper and more saline Central Bay adjacent to the City of San Francisco. Here, strong tidal currents create a highly dynamic bottom consisting of large sand waves that reverse direction on each tide (Rubin and McCulloch 1979). The benthic community is composed largely of species that are found in sand sediments along the outer coast (Storrs et al. 1965; Liu et al. 1975; Nichols 1979). Islands and other rock outcrops in Central Bay are inhabited by hard-substrate organisms with marine affinities, as well as by the cosmopolitan bay mussel Mytilus edulis.

South of San Francisco, the species found in San Pablo Bay are joined, in the subtidal mud areas, by high densities of the large tube-dwelling polychaete Asychis elongata. In the intertidal and shallow subtidal reaches of South Bay, Gemma gemma, Ampelisca abdita, and Streblospio benedicti are the overwhelming numerical dominants, although large numbers of individuals of other species occasionally appear (Nichols and Thompson 1985a). While much less abundant than Gemma, Ampelisca, and Streblospio, the mollusks Macoma balthica, Mya arenaria, and Ilyanassa obsoleta often represent the bulk of benthic invertebrate biomass (Nichols 1979; Thompson and Nichols 1981). Where the bottom is covered with shell deposits (Figure 9; remnants both of the

early Pacific oyster industry and the ancient deposits of the native oyster, Ostrea lurida; Hart 1966), invertebrates associated with hard bottoms, such as Crepidula spp., Urosalpinx cinerea, Mogula manhattensis, Musculista senhousia, and unidentified hydrozoans, cheilostome bryozoans, and acontiate anemones, are found. Tapes philippinarum is also common in the shelly deposits.

2.2.2 Baywide Patterns of Macroinvertebrate Biomass

The only synoptic survey of macroinvertebrate biomass (sampled twice during 1973; Nichols 1979; Thompson and Nichols 1981) demonstrated (1) the major contribution of mollusks to total invertebrate biomass everywhere in the bay, and (2) the concentration of greatest total biomass in South Bay (Table 1).

The principal contributors to biomass throughout much of the bay are the mollusks Tapes philippinarum, Musculista senhousia, Macoma balthica, Mya arenaria, Gemma gemma, and Ilyanassa obsoleta. In addition, the large tube-dwelling polychaete Asychis elongata is a major contributor to total biomass in the muddy subtidal areas of South Bay (Nichols 1979). Because sampling during this single baywide survey was conducted only twice during one year, meaningful seasonal comparisons are not possible.

2.3 INTRODUCED INVERTEBRATES

Of all the common benthic species listed above, only the polychaete Glycinde sp. (a species belonging to the G. armigera/polygnatha complex), and the bivalve mollusks Macoma balthica and Mytilus edulis are natives. The others were accidentally or intentionally introduced (Carlton 1979a,b). Moreover, there is developing evidence from electrophoretic studies that Macoma balthica may also be introduced: they are genetically much more similar to U.S. east coast M. balthica than they are to those collected from Coos Bay, Oregon (B.W. Meehan, Virginia Institute of Marine Science; pers. comm.). However, because its native/introduced status has not been formally resolved, we continue to refer in this profile to M. balthica as a native species.

The immigrants who flocked to the west coast of the United States during the Gold Rush of the late 1840's and 1850's brought with them a taste for fresh oysters, but did not care for the dark, strong-tasting meat of the local oyster Ostrea lurida. Live oysters were imported to San Francisco by ship from Mexico, the Pacific Northwest, and Japan. Shells of the various species can still be found on bay intertidal flats (Figure 11). With the completion of the transcontinental railroad in 1869, large-scale shipment of

Table 1. Weight (g/0.1 m²) and percent (%) of total sample wet weight for Mollusca, Annelida, Arthropoda, and all other phyla combined; data are averages of 4 to 13 stations in each region of the bay. Samples were collected during January-February (winter) and during August (summer) 1973 (Thompson and Nichols 1981).

| Location | Mollusca | | Annelida | | Arthropoda | | Other Phyla | | Total | |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-------------|-------------|
| | winter g (%) | summer g (%) | winter g (%) | summer g (%) | winter g (%) | summer g (%) | winter g (%) | summer g (%) | winter g | summer g |
| Suisun Bay | 13(81) | 4(67) | 3(19) | 1(17) | <1(<1) | <1(<1) | <1(<1) | 1(17) | 16 | 6 |
| San Pablo Bay | 36(90) | 56(88) | 2 (5) | 1 (2) | <1(<1) | 2 (3) | 1 (2) | 4 (6) | 40 | 64 |
| Central Bay | 41(70) | 6(14) | 7(12) | 13(31) | 1 (2) | 2 (5) | 9(15) | 21(50) | 59 | 42 |
| Upper South Bay | 466(85) | 332(83) | 64(12) | 49(12) | 5 (1) | 6 (2) | 13 (2) | 15 (4) | 549 | 402 |
| Lower South Bay | 81(92) | 191(92) | 6 (7) | 8 (4) | <1(<1) | 2 (1) | 1 (1) | 6 (3) | 88 | 207 |

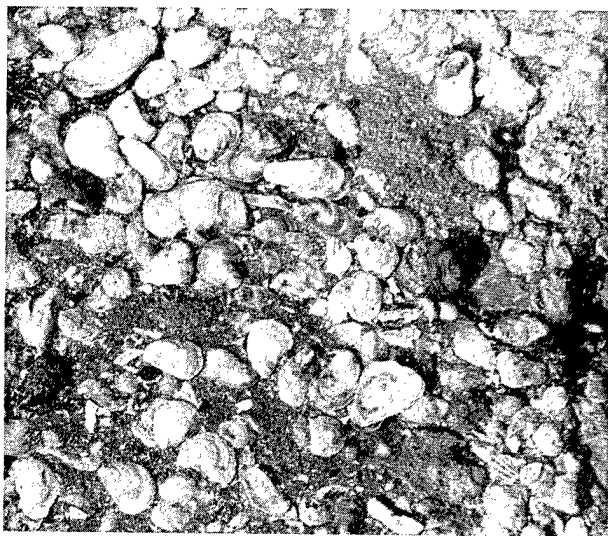


Figure 11. Accumulated oyster shells of assorted species on a South Bay mudflat.

mature eastern oysters, Crassostrea virginica, and, later, seed oysters for maturing on the mudflats of coastal bays, became possible. An average of 100 carloads of seed oysters were shipped each year between 1875 and 1910. By the late 1890's, oysters became California's most valuable fishery product (Barrett 1963).

The eastern oyster never became naturalized in San Francisco Bay (transplanted adults failed to produce sufficient young), but its large-scale introduction contributed to one of the most significant bay-wide ecological changes recorded since. Species associated with the oyster in its native habitat became unintentional fellow travelers on the transcontinental trip and subsequently established themselves in San Francisco Bay with phenomenal success. Carlton, in his review (1979b) of species introductions in the bay, commented that "A single oyster shell may have upon it representatives of 10 or more invertebrate phyla, comprising dozens of species, and these numbers can be greatly increased when oysters are packed together for shipment with associated clumps of mud and algae, and with water pockets in empty valves used as cultch." Biologists recorded the appearance of many of these exotic species during the period of oyster importation (Figure 12). However, the enormous significance of species introductions,

including those associated with the oyster industry as well as those attached to or bored into ship hulls or contained in ship ballast and subsequently released to the bay, was not realized for nearly 100 years (Carlton 1979a,b). In total, about 100 species of exotic estuarine/marine invertebrates have become established. These include the edible soft-shelled clam Mya arenaria and the Japanese littleneck clam Tapes philippinarum--the only two mollusk species represented today in the bay sport fisheries--and such pest species as the shipworm Teredo navalis and the oyster drill Urosalpinx cinerea. Now, nearly all the common macroinvertebrate species present on the inner shallows of the bay are introduced (Nichols 1979; Nichols and Thompson 1985a). Some of these species, such as the amphipod Ampelisca abdita, are abundant nearly everywhere in the bay (Figure 13). The tidal freshwater waterways of the lower Sacramento and San Joaquin Rivers and Delta, as well as of California's irrigation canals, contain huge numbers of the introduced freshwater clam Corbicula fluminea.

Introduced invertebrates are evident at the edge of the bay to even the most casual observer. The bayward edges of the Salicornia/Spartina marshes throughout the bay are populated by the eastern ribbed mussel Geukensia demissa (= Ischadium demissum, Modiolus demissus) (Figure 14), and the slopes formed by ongoing erosion of the marsh edge in many South Bay and San Pablo Bay locations (Atwater et al. 1979; Carlton 1979b) are perforated with (and ultimately destroyed by) the burrows of the introduced isopod Sphaeroma quoyana (Figure 15). At the base of these slopes and in tidal channels the mudsnail Ilyanassa obsoleta resides in great numbers. While it is typically found in relatively small numbers on open South Bay mudflats, Ilyanassa is occasionally extremely abundant (Figure 16). At the base of riprap dikes and breakwalls, particularly where the sediments contain some cobbles and sand, the Japanese littleneck clam Tapes philippinarum is easily found by clam diggers.

Total mollusk biomass is dominated by introduced species in all regions of the bay except Central Bay, where a variety of native marine species predominate, and in Suisun Bay, where Macoma balthica normally predominates (Figure 17; Thompson and Nichols 1981). If, as mentioned above,

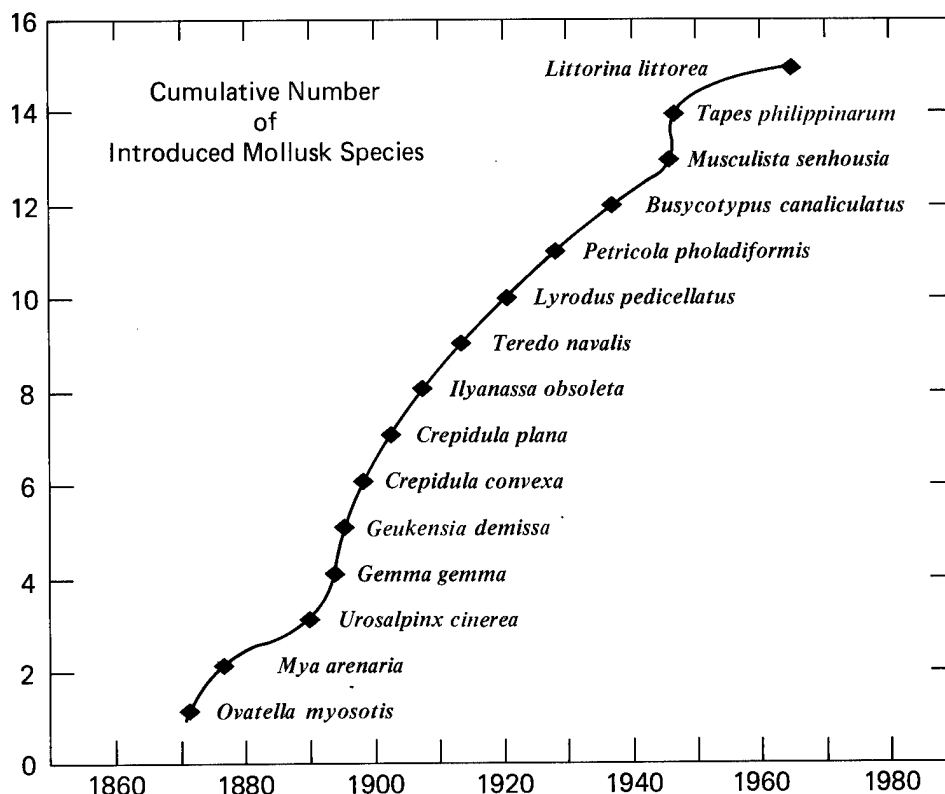


Figure 12. Cumulative number of introduced mollusks by date of discovery (adapted from Nichols et al. 1986; derived from data in Carlton 1979b).

Macoma balthica proves to be another introduced species, the percentages shown in Figure 17 for native species in Suisun, San Pablo, and South Bays would be greatly diminished.

Accidentally introduced species may have thrived in San Francisco Bay in part because the bay, like other Pacific coast estuaries, contained relatively few native species as compared with the estuaries on the U.S. east coast (Jones 1940, Hedgpeth 1968, Carlton 1979a,b). This was the case, apparently, because of the geologic youth and geographic isolation of west coast estuaries (Figure 2): a diverse local fauna had apparently not yet evolved prior to the introduction of species (Hedgpeth 1968). The predominance of a single habitat type (soft mud) over wide areas of the bay may also have restricted the number of species that were established there. Sources of potential colonizing species not commonly a part of the soft-mud community may have been too small or too far removed spatially from

the bay's mudflats to be effective sources of colonizers (Nichols and Thompson 1985a).

The success of the introduced species may also be related to their flexible lifestyles. The introduced species are well known in estuaries of the eastern United States as opportunistic colonizers of underexploited or disturbed habitats (Nichols and Thompson 1985a). They have short life spans, produce large numbers of young, are tolerant of a wide range of salinity, temperature, and substrate type, and can be readily dispersed around the bay by tide- and wind-driven currents. The large seasonal variations in river inflow, with consequent variations in salinity, contribute to an instability of the benthic environment that enhances the success of the opportunists rather than longer lived "equilibrium" species (as in McCall 1977). The same hardiness that permitted the eastern species to survive the long transcontinental train rides

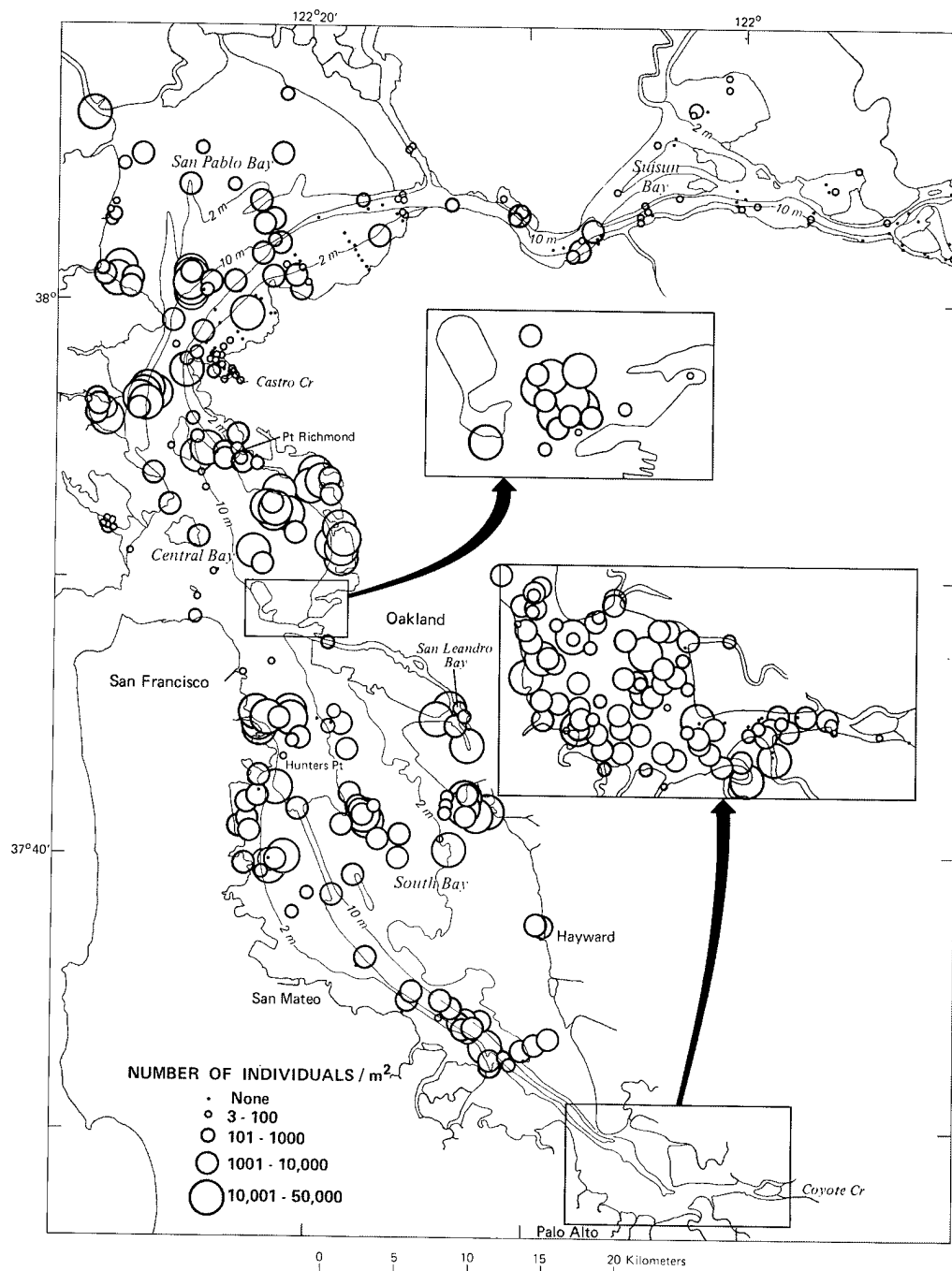


Figure 13. Distribution and abundance of *Ampelisca abdita* (= *Ampelisca milleri* = *Photis californica* in earlier local studies; Carlton 1979a,b) (from Hopkins 1986).



Figure 14. The introduced eastern ribbed mussel, *Geukensia demissa*, at the edge of a *Spartina foliosa* marsh in South Bay.

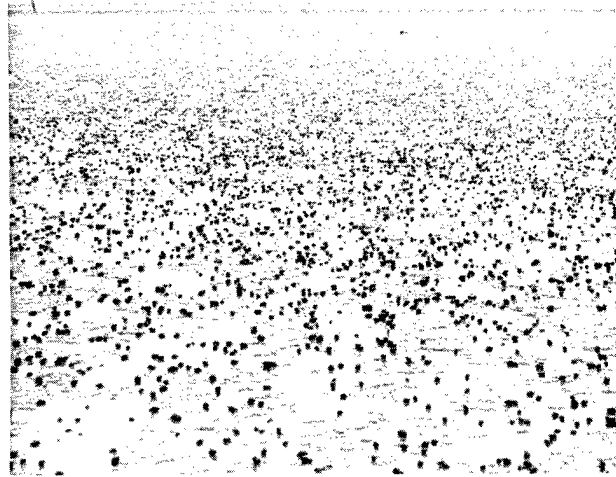


Figure 16. An unusually high concentration of the introduced mudsnail *Ilyanassa obsoleta* on a South Bay mudflat, November 1985.

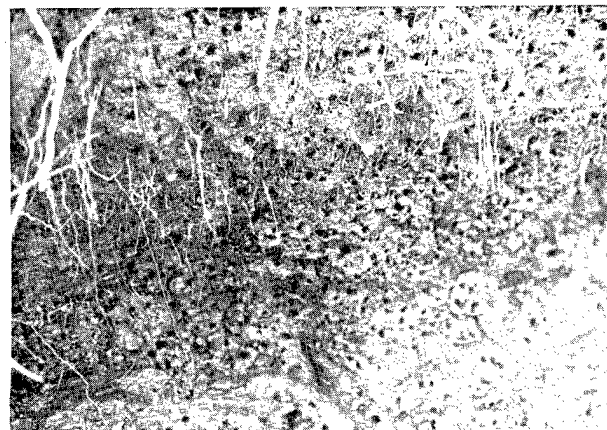
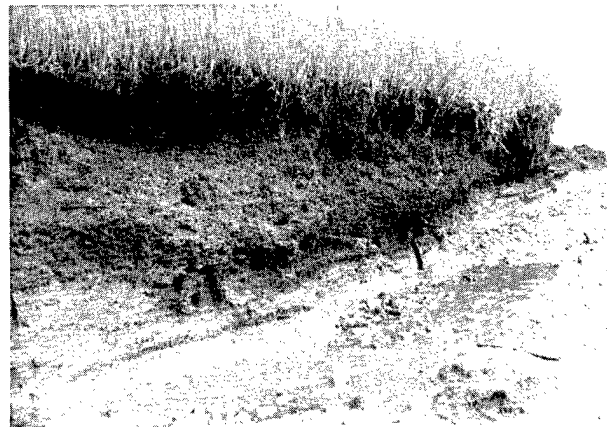


Figure 15. Eroding edge of a San Francisco Bay marsh, perforated by burrows of the introduced isopod *Sphaeroma quoyana*.

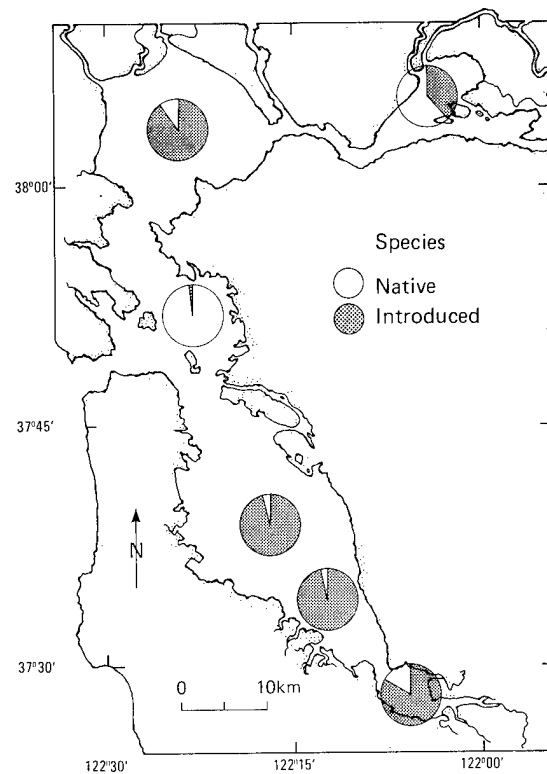


Figure 17. Proportions of introduced and native species relative to total biomass (wet weight) of mollusks in major subareas of San Francisco Bay (averages from four to seven stations per subarea, three samples per station). These proportions assume that *Macoma balthica* is a native species, an assumption that may be invalid; see text.

probably insured their successful establishment in San Francisco Bay.

We do not know how the introduced species affected the native benthic community, but they may have altered the distribution and survival of some of their native counterparts. In one documented case (Race 1982), the range of the native hornsnail Cerithidea californica is restricted mainly to marsh pannes (Figure 18) by competitive interaction with and predation by the introduced mudsnail Ilyanassa obsoleta. It is likely that, before Ilyanassa was introduced,



Figure 18. The salt-panne habitat of the native hornsnail Cerithidea californica.

Cerithidea was found on the open mudflats of the bay. It is also possible that before the introduction of Ampelisca abdita, Macoma balthica was the most abundant invertebrate of the bay's intertidal mudflats (Section 3.2.3). If so, it may have provided the most important source of nutrition for migratory shorebirds.

2.4 PREDATORS ON THE BENTHOS

The importance of predation on the bay's clams and oysters has been recognized since the early days of shellfish harvesting in the bay (Bonnot 1932a, 1935; Barrett 1963). The beds of oysters (Ostrea lurida) imported from the State of Washington during the 1850's were fenced with stakes to keep out predators, particularly rays (Barrett 1963). Bonnot (1932a) noted that "The stingrays and flounders eat vast quantities of the [soft-shell clam Mya arenaria]. The stingrays will dig and eat the whole clam. The flounders bite off their siphons." The predators mentioned by Bonnot are probably the bat ray Myliobatis californica and the starry flounder Platichthys stellatus which, with the leopard shark Triakis semifasciata, may be responsible for some of the discernible feeding depressions on mudflats (Figure 19). The practice of shellfish bed fencing to prevent these

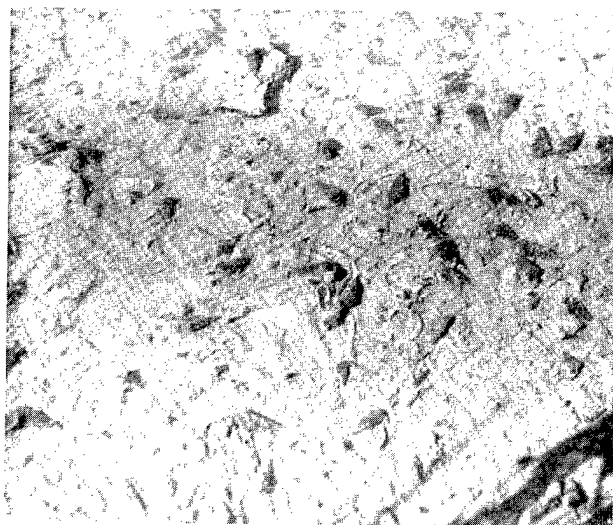


Figure 19. Feeding depressions (about 15 cm in diameter), probably made by the bat ray (Myliobatis californica), known to feed on the mudflats at high tide.

species and others from depleting the beds continued throughout the period of oyster growing and soft-shell clam harvesting (Chapter 6). Native epibenthic invertebrates such as the Dungeness crab Cancer magister, the bay shrimp Crangon spp., the shore crab Hemigrapsus oregonensis, and the channeled whelk Busycotypus canaliculatus are also important predators, depending on location within the bay and time of year.

Studies of bay fishes, crustaceans, and birds (e.g., Heubach et al. 1963, Ganssle 1966, Radtke 1966, Stevens 1966, Boothe 1967, Thomas 1967, McKechnie and Fenner 1971, Daniels and Moyle 1983 for fishes; Russo 1975 for elasmobranchs; Recher 1966 for birds; Wahle 1985 for shrimp) often have included observations of stomach contents. While not quantita-

tive, these studies show clearly that the benthos is a major source of nutrition. Use of such studies for purposes of determining precise feeding habits and rates is limited, however, in that partly digested stomach contents may not necessarily provide a true picture of food selection. Recher (1966), for example, showed from shorebird gizzard contents that prey selection was species specific (Table 2), and that the large polychaete Nereis succinea was the apparent preferred food item for many species. He noted, on the other hand, that while clams represented only a small percentage of stomach contents of long-billed shorebird species, these birds were routinely observed to extract clams (Macoma balthica and Mya arenaria?) from the mud. Small soft-bodied animals such as Streblospio benedicti and other polychaetes would probably be overlooked in analyses of stomach contents as well.

Table 2. Percent composition of food items occurring in the gizzards of shorebirds collected at Palo Alto (Recher 1966).

| Bird species (with number of gizzards analyzed) | | | | | | | | | | |
|---|-------------------------|--------------------------|------------|----------------|-----------------------|-------------------------|---------------------------|----------|--------------------|-------------|
| Invertebrates recovered | Semipalmated Plover (3) | Black-bellied Plover (3) | Avocet (9) | Dowitcher (27) | Least Sand-piper (38) | Western Sand-piper (78) | Red-Backed Sandpiper (46) | Knot (3) | Marbled Godwit (9) | Willet (16) |
| Amphipod species | - | - | 4.0 | - | 21.1 | 8.6 | 8.9 | - | - | - |
| <u>Gemma gemma</u> | 2.8 | 12.7 | 52.0 | 6.4 | 5.3 | 8.6 | 2.4 | 55.3 | 6.2 | 44.6 |
| <u>Nereis succinea</u> | 94.5 | 16.4 | 16.0 | 71.4 | 5.3 | 8.6 | 70.0 | 44.0 | 76.0 | 4.6 |
| Ostracod species | 0.5 | - | 4.0 | 9.6 | 57.8 | 62.8 | 9.7 | - | - | - |
| <u>Ilyanassa obsoleta</u> | | | | | | | | | | |
| <1/4 inch | 2.2 | 1.8 | 24.0 | 7.4 | 10.5 | 11.4 | 5.8 | - | 2.5 | 9.9 |
| >1/4 inch | - | 65.5 | - | 2.1 | - | - | 1.6 | 0.7 | 8.7 | 33.2 |
| <u>Geukensia demissa</u> | - | - | - | - | - | - | - | - | - | 0.8 |
| <u>Mya arenaria</u> and <u>Macoma balthica</u> | | | | | | | | | | |
| | - | 3.6 | - | 3.1 | - | - | 1.6 | - | 6.6 | 3.8 |
| <u>Hemigrapsus oregonensis</u> | - | - | - | - | - | - | - | - | - | 3.1 |
| Average number of items per gizzard | 137 | 55 | 25 | 94 | 38 | 35 | 121 | 159 | 195 | 132 |

2.5 INVERTEBRATE FEEDING

2.5.1 Feeding Modes

There has been, to our knowledge, only one study of invertebrate feeding in the San Francisco Bay Estuary: Foe and Knight's (1985a, 1986) study of Corbicula fluminea in the tidal freshwater region of the estuary. Life histories and feeding modes of the common invertebrates of San Francisco Bay must, therefore, be inferred from studies of these species in other United States estuaries. Feeding modes (the mechanism of food transport from the environment into the organism; Fauchald and Jumars 1979), while highly dependent on the functional morphology of each species, are also locally influenced by substrate type as well as sources and rates of food supply. Thus, our characterization of the bay's benthic invertebrate feeding modes (Table 3) is based on observations of local populations, habitat type, and potential sources of food as well as on published studies of the same species elsewhere.

It is apparent from Table 3 that, with the exception of some polychaetes, the common species of San Francisco Bay macroinvertebrates are filter feeders or surface deposit feeders (including surface grazers). Moreover, the group of species representing the bulk of invertebrate biomass--the bivalve mollusks--is composed entirely of filter feeders, although Macoma balthica is a surface deposit feeder as well as a filter feeder (Hummel 1985): Macoma feeding traces are nearly always prominent on the bay mudflat surfaces (Figure 20).

While definitive studies have not been conducted, the most readily apparent food sources for this abundance of filter feeders and surface deposit feeders are probably phytoplankton and benthic microalgae. Because the estuary is shallow and well mixed, phytoplankton in the water column is directly available to filter feeders on the bottom. Cloern (1982) concluded that the benthos limits the size of phytoplankton blooms in South Bay. Benthic grazing may also have been responsible for the unusually low levels of

Table 3. Reported feeding modes of common soft-bottom macroinvertebrates found in San Francisco Bay.

| Species | Filter feeders | Surface deposit feeders | Subsurface deposit feeders | Grazers, carnivores, omnivores | References |
|--------------------------------|----------------|-------------------------|----------------------------|--------------------------------|--------------------------|
| Polychaeta | | | | | Fauchald and Jumars 1979 |
| <u>Asychis elongata</u> | | | X | | " |
| <u>Capitella</u> sp. | | X | X | | " |
| <u>Heteromastus filiformis</u> | | X | X | | " |
| <u>Glycinde</u> sp. | | | | X | " |
| <u>Nereis succinea</u> | | | | X | " |
| <u>Polydora</u> spp. | X | X | | | " |
| Crustacea | | | | | |
| <u>Ampelisca abdita</u> | X | X | | | Mills 1967 |
| <u>Corophium</u> spp. | X | X | | | Newell 1970 |
| <u>Sphaeroma quoyana</u> | X | | | | Rotramel 1972 |
| Mollusca | | | | | |
| <u>Corbicula fluminea</u> | X | | | | Foe and Knight 1985a |
| <u>Gemma gemma</u> | X | | | | Sellmer 1967 |
| <u>Ilyanassa obsoleta</u> | | | | X | Curtis and Hurd 1981 |
| <u>Geukensia demissa</u> | X | | | | Kuenzler 1961 |
| <u>Macoma balthica</u> | X | X | | | Hummel 1985 |
| <u>Musculista senhousia</u> | X | | | | Morton 1974 |
| <u>Mya arenaria</u> | X | | | | Newell 1970 |
| <u>Tapes philippinarum</u> | X | | | | Langton et al. 1977 |

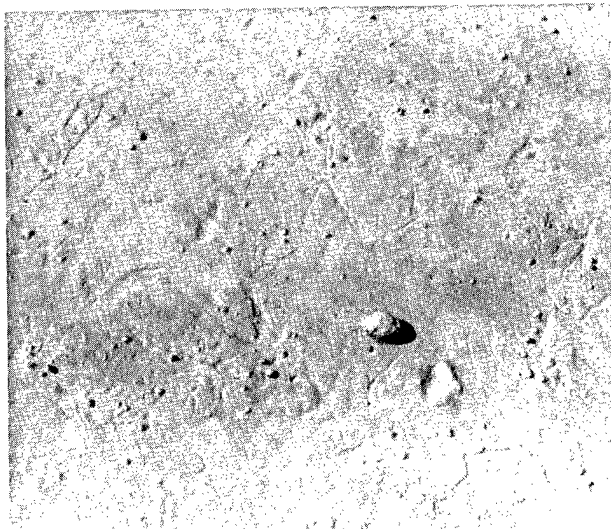


Figure 20. *Macoma balthica* feeding traces, with the mudsnail *Ilyanassa obsoleta* for scale (photograph courtesy of D.R. Hopkins).

phytoplankton in Suisun Bay during the 1976-77 drought (Nichols 1985b). Further, because approximately 45% of the bay's surface area at high tide is covered by less than 2 m of water, a depth equivalent to the bay's average photic depth, benthic microalgae are also a potential major source of food (Chapter 4).

A recent study of growth in *Macoma balthica* (Thompson and Nichols in press) shows that the timing and rate of growth are related to the timing and magnitude of blooms in either the phytoplankton or phytobenthos or both (Section 3.1.2). Most of the other benthic invertebrate species found in high abundance, e.g., *Ampelisca abdita*, *Streblospio benedicti*, and *Gemma gemma*, as well as the large mollusks *Mya arenaria*, *Geukensia demissa*, *Mytilus edulis*, *Musculista senhousia*, and *Tapes philippinarum*, also directly consume microalgae, either by filtering water or selectively feeding at the sediment surface. The mudsnail *Ilyanassa obsoleta*, a surface grazer, is known to feed directly

on benthic microalgae or sedimented phytoplankton as well as on live animals and carrion (Curtis and Hurd 1981).

River-borne organic detritus, decaying vascular plants and associated microbes and epiphytes washed from the marshes, wastes from sewage-treatment plants (Chapters 4 and 5), and microbes and meiofauna living in bottom sediments also contribute to the diet of filter and deposit feeders (Section 4.2). As yet, however, we have no understanding of their quantities, rates of supply, or relative importance to benthic feeding.

2.5.2 Benthic Food Web

There have been no studies of food web interactions within the San Francisco Bay benthos. Nonetheless, our knowledge of the behavior of individual species (supplemented by studies in other estuaries) is sufficient to describe a probable food web of the shallow benthos of the bay: microalgae growing both in the shallow water column and on the sediment surface (with considerable overlap between the two "communities"), mixed and transported across the intertidal or shallow subtidal mudflats by wind- and tide-induced currents, are directly available to suspension or surface deposit feeding invertebrates. Thus, there is an immediate transfer of food energy from microalgae to invertebrates. The benthic invertebrates are, in turn, eaten by such large consumers as shorebirds, demersal fishes, elasmobranchs, juvenile Dungeness crabs in the northern reaches of the bay (Section 3.3.3), and by human clam diggers (Chapter 6). This simple, efficient food web that links microalgae directly with clams without an intermediate pelagic consumer link--much like that of an aquaculture system--should be appropriate for commercial shellfish growing (Chapter 6). Whether microbe-coated sediment particles are an equally or more important source of nutrition for the mudflat inhabitants remains to be determined.

CHAPTER 3. MACROFAUNAL COMMUNITY DYNAMICS

Estuarine benthic species undergo marked changes in abundance over a variety of time scales (Nichols 1985a). Most changes are associated with species-specific seasonal patterns of recruitment, growth, and mortality. Other equally important changes result from predictable or unpredictable changes in the estuarine habitat that occur over time scales ranging from tidal cycles to years (e.g., responses to the seasonality of river flow or predation, or to climatic events and trends). A few changes reflect historic events that permanently altered communities, and still others represent modern anthropogenic influences (Chapter 5).

3.1 SEASONAL PATTERNS IN THE BENTHIC COMMUNITY

The results from benthic surveys that include sampling at fixed sites through time show that abundances of individual species vary widely between seasons and from year to year (e.g., Figure 21).

3.1.1 Abundance Changes

Little is known about the mechanisms that trigger reproductive activity or that affect recruitment success in the bay's benthic species populations. Nonetheless, some of the mechanisms contributing to major abundance fluctuations have been identified in quantitative surveys and in studies of reproductive activity and life history of several numerically prominent species (Nichols and Thompson 1985a). We know little about the natural history of species other than these few.

Generally, macrobenthic invertebrates at temperate and higher latitudes increase in abundance in patterns associated with the annual temperature cycle. In San

Francisco Bay, the small and highly abundant amphipod Ampelisca abdita demonstrated year-to-year consistency, over a 10-year period, in the timing of abundance fluctuations, with peak abundance occurring in October of most years (Figure 22; Nichols and Thompson 1985a). This consistency may reflect the fact that this species has two generations each year--a small overwintering generation comprising juveniles and subadults that mature in spring, and a subsequent spring generation that rapidly matures and produces the summer-autumn generation. The overwintering individuals come from this latter generation (Mills 1967; Kinnetic Laboratories, Inc. 1983; Nichols and Thompson 1985a).

The timing of recruitment of the northern temperate bivalve Macoma balthica is also reasonably predictable. In San Francisco Bay, recruitment occurs mostly during two periods each year: in late winter to early spring and again in late summer to early autumn (Nichols and Thompson 1982), although the relative importance of spring and autumn recruitment varies from location to location within the bay (Thompson and Nichols unpubl. data). In the absence of cold winters (Macoma is more typically found at higher latitudes), temperature may not be the major stimulus for reproductive development in San Francisco Bay. The timing of food availability (associated with phytoplankton and phytobenthos blooms) also may be an important factor in the reproductive maturation cycle (Thompson unpubl. ms.).

Although the timing of Macoma abundance peaks at one South Bay study site is somewhat predictable, the maximum size of the population during any year is not (Nichols and Thompson 1985a): in some years Macoma is extremely abundant, while in others it is nearly absent (Figure 21).

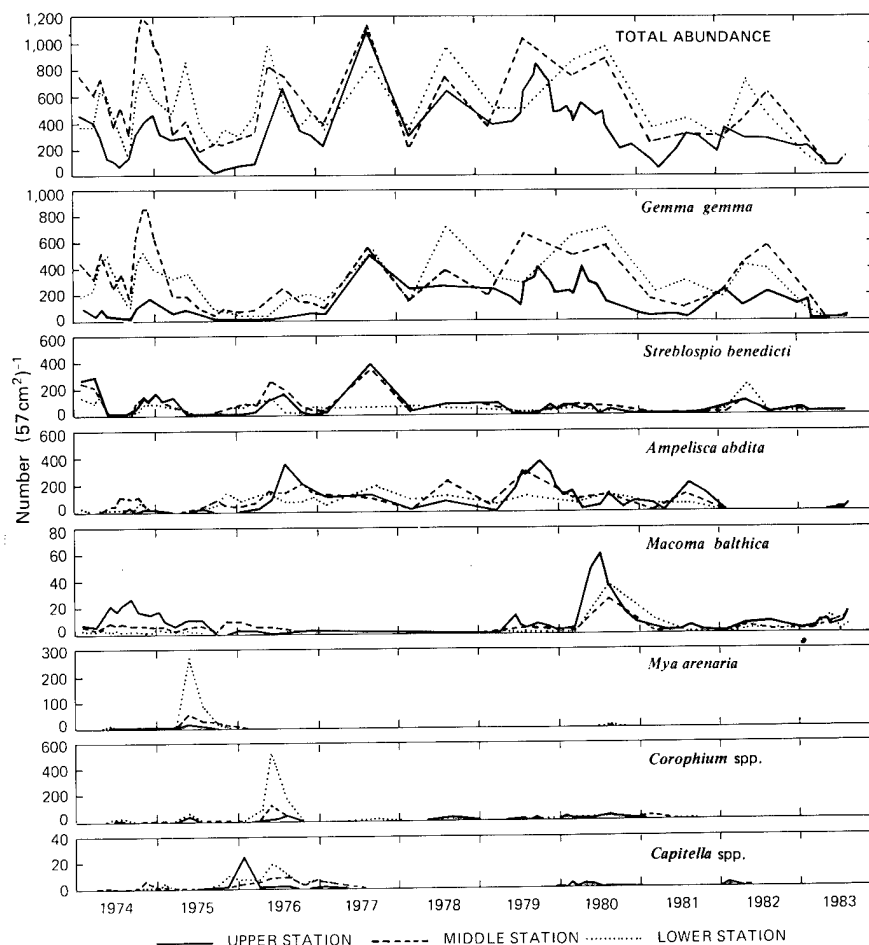


Figure 21. Abundance of the macrofauna collected in core samples at three stations on an intertidal mudflat at the Palo Alto study site (Figure 4), including three numerically dominant species (*Gemma*, *Streblospio*, *Ampelisca*), the species that accounts for the largest percentage of biomass (*Macoma*), and three irruptive species (*Mya*, *Corophium*, *Capitella*) (from Nichols and Thompson 1985a).

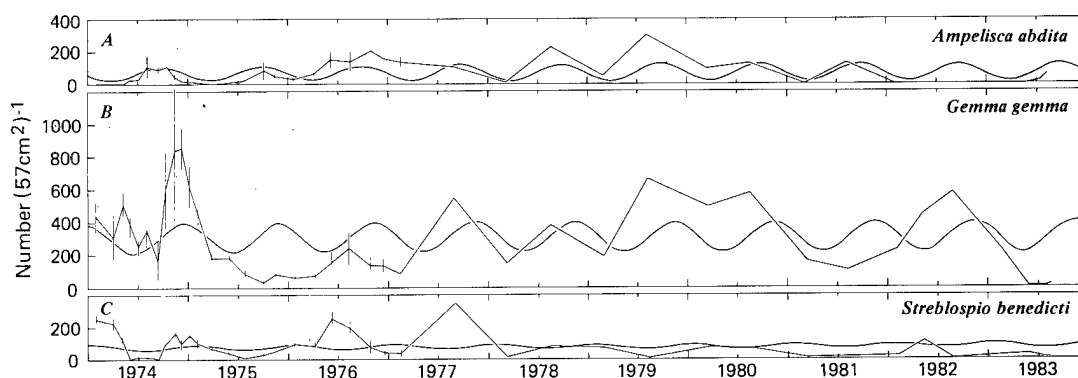


Figure 22. Abundance (average ± 1 s.d., 1974-76) of three numerically dominant mudflat species over a 10-year period (straight lines), and computed average annual cycles from least-squares regression of the data (curvilinear lines) (from Nichols and Thompson 1985b).

The large year-to-year differences could result from variable predation on adults by birds, rays, and fishes; variable predation on planktonic larvae; variation in the number of larvae in the water column available for settling; variations in the number of larvae that successfully settle to the sediment surface; or in the presence or absence of potentially interfering species once they have settled (Section 3.2).

Abundance fluctuations among other common bay invertebrates seem much more random. The timing of annual abundance peaks of two numerically dominant species, the clam Gemma gemma and the polychaete Streblospio benedicti, is highly variable from year to year (Figure 22; Nichols and Thompson 1985a).

The climate of the San Francisco Bay region, moderated by mild winters and by the influx of colder, upwelled water from offshore during the summer, maintains bay water temperatures within a narrow range. Such a temperature regime may permit greatly increased reproductive flexibility in some species. Gemma and Streblospio, like Ampelisca, are brooders, but their females remain reproductively active during much of the year (Jones 1961; Thompson 1982; Nichols and Thompson 1985a). Additionally, strong water mixing within and between embayments probably contributes to bay-wide dispersal of water-borne larvae, juveniles, and adults of these small species. Thus, the potential for rapid colonization of available substrates throughout much of the year is greatly enhanced (Nichols and Thompson 1985a). Successful recruitment, nonetheless, may depend on local conditions (physical conditions at sediment surface, presence of competitors or predators, etc.) at the time of larval release.

All of these factors (temperature, water column mixing, sediment character, predation, species interference) together undoubtedly contribute to extreme year-to-year variability observed in the timing of population increases, and render short-term assessments of community structure for the purpose of environmental quality analysis (Chapter 5) relatively useless.

3.1.2 Seasonal Growth

Field and experimental studies worldwide have shown that rate of growth

in benthic invertebrates also varies markedly with time. Many studies (reviewed in Nichols and Thompson 1982) have shown that the clam Macoma balthica typically grows most rapidly during a brief period in spring, typically in association with a temperature-dependent seasonal cycle of reproductive development (de Wilde 1975) and the availability of food (Beukema et al. 1977; Christensen and Kannevorff 1985). Although Macoma in San Francisco Bay grows to some degree throughout the year, most of the growth in South Bay populations takes place during a brief period in spring (Figure 23) coincident with the spring phytoplankton and benthic microalgal blooms (Nichols and Thompson 1982, 1985b). Growth rates are also higher in San Francisco Bay than in any other location, worldwide, apparently because of the warmer water temperature (Nichols and Thompson 1982).

Growth in bay populations of the amphipod Ampelisca abdita, the clam Gemma gemma, the isopod Sphaeroma quoyana, the mussel Geukensia demissa, the snail Cerithidea californica, and the freshwater clam Corbicula fluminea is also strongly focused in spring or summer (Schneider 1976; Langlois 1980; Race 1981; Thompson 1982; Kinnetic Laboratories, Inc. 1983; Foe and Knight 1985a).

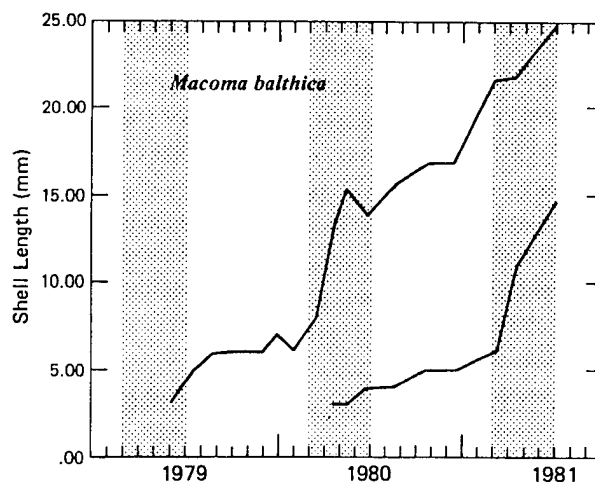


Figure 23. Average length of individuals in two year classes (recruited in 1979, 1980) of *Macoma balthica* (from Nichols and Thompson 1985b).

A more recent study, in which growth of Macoma balthica was examined experimentally at four different locations in San Francisco Bay, has confirmed the existence of a strong link between maximum clam growth and seasonal peaks in microalgal biomass. Furthermore, the timing of microalgal-biomass and clam-growth peaks varied depending on location within the bay (Thompson and Nichols in press).

3.1.3 Seasonal Predation

The effects of predation by representatives of other groups (e.g., birds, fish, crabs, etc.) on seasonal distribution and abundance patterns have been demonstrated experimentally in many studies around the world (e.g., Peterson and Peterson 1979; Baird et al. 1985). However, with the exception of Recher's (1966) study of shorebird distributions and stomach contents at one intertidal site in South Bay (Table 2), little quantitative information exists on the distribution, abundance, and feeding behavior of large predators from which seasonal estimates of predation losses could be made. Similarly, only one study of invertebrate predators has been conducted in San Francisco Bay. In that study Race (1982) found that the introduced snail Ilyanassa obsoleta competitively displaced the native snail Cerithidea californica from its preferred summer habitat and preyed upon its eggs.

The distributions of some predators are strongly seasonal and, as a result, should contribute to seasonal patterns in invertebrate abundance. As examples, migratory shorebirds that feed on many of the common intertidal mudflat invertebrates are more abundant during the autumn and winter months (Recher 1966), while the bat ray Myliobatis californica is most prevalent during summer (Aplin 1967). A long-term baywide study of fish distributions and stomach contents, now in its sixth year (Armor and Herrgesell 1985), should begin to provide pertinent information on spatial and temporal patterns of feeding on the benthos by fish and elasmobranch predators and on species-specific food preferences.

3.2 APERIODIC PATTERNS OF ABUNDANCE

The absence of predictable patterns in the abundance of many benthic inver-

tebrates of the bay and the rapidity of community changes suggest that stochastic processes contribute markedly to observed variability.

3.2.1 Effects of Environmental Perturbations

The 10-year study of an intertidal benthic community in South Bay (Section 3.1.1) revealed rapid changes in individual species abundances (Figure 21) that, with respect to our understanding of species life histories, are largely unpredictable. While the factors contributing to these changes seldom are clearly understood, periodic or aperiodic disturbances of the environment are implicated (Nichols and Thompson 1985a,b). As an example, the annual decline in Ampelisca during autumn and winter at any site is assumed to be the result of natural autumn-winter mortality following reproduction. Several data sets, however, suggest a connection between observed rapid declines and inundation by low-salinity surface water and the possibility of mass migration of animals away from inundated sites to more saline, deeper or down-estuary regions of the bay (Nichols and Thompson 1985b).

Similarly, many of the most dramatic between-year community changes may be attributable to extreme deviations in the physicochemical environment from long-term norms that, in turn, may influence the timing and success of recruitment of new individuals to the community or the survival of individuals already established. Interannual variations in river flow into the estuary have a particularly strong effect. Extremely low river inflow from the Sacramento-San Joaquin River system during two successive winters (1976 and 1977) resulted in steadily increasing salinity and an increase in both species diversity and abundance in Suisun Bay at the upper end of the estuary (Figure 24). It is assumed that larvae and juveniles of estuarine benthic species normally found only downstream of Carquinez Strait (Figure 4) were carried upstream to Suisun Bay by gravitational circulation and tidal currents. The temporarily enlarged benthic community (Figure 25), comprising several filter feeders, may have contributed to the equally unusual decline in phytoplankton biomass in Suisun Bay at the same time (Nichols 1985b). The return of normal river flow and reduced salinity at

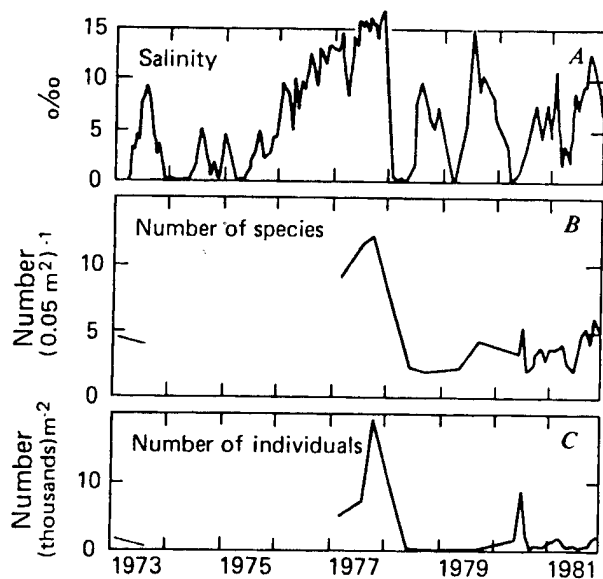


Figure 24. Salinity, mean number of macrofauna species, and mean number of individuals at a shallow site (Figure 4, site D7) in Suisun Bay (adapted from Nichols 1985b); data from California Department of Water Resources 1986.

the end of 1977 quickly eliminated these transient species populations from Suisun Bay (Figure 24).

At the opposite extreme, high river inflow "events," such as occurred during the winter and spring of 1982 and again in 1983, cause a rapid lowering of salinity throughout the bay. Inundation by brackish or freshwater during these events resulted in a decline of abundance within the intertidal benthic community and the near-elimination of the amphipod *Ampelisca abdita* (Figure 26). Two years passed following the 1982 period of high river inflow before *Ampelisca* regained its numerical prominence (Nichols and Thompson 1985a). The Japanese littleneck clam *Tapes philippinarum* also declined in 1982 and again in 1986 following unusually heavy rainfall and runoff and the subsequent siltation of clam beds (T.O. Moore, Jr., California Department of Fish and Game; pers. comm.). Coincident with the inundation by low-salinity water during the winter of 1982 was the deposition of fine terrigenous mud over the intertidal mudflats throughout the bay (and probably the subtidal as well) and thick layers (up to 15 cm) of sand on top

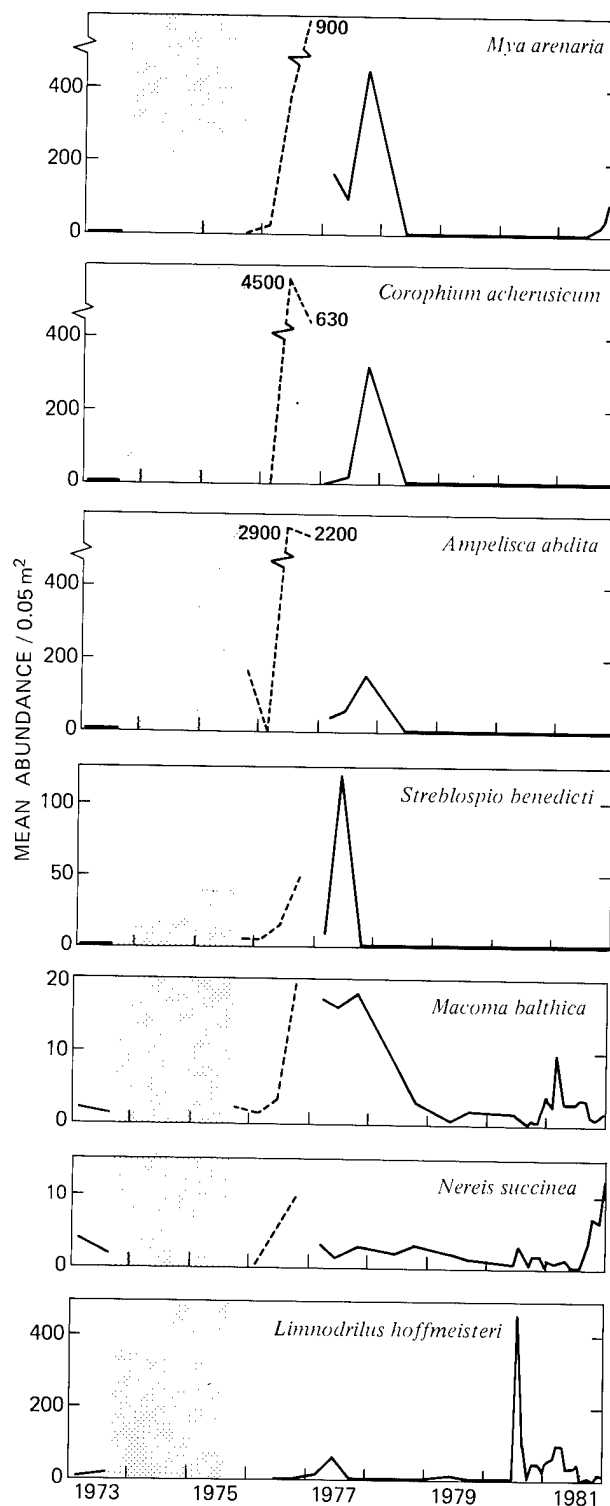


Figure 25. Average abundance of numerically abundant species at sites D6 (dashed line) and D7 in Suisun Bay (Figure 4); data as in Figure 24 above (adapted from Nichols 1985b); no data between late 1973 and late 1975 (stippled area).

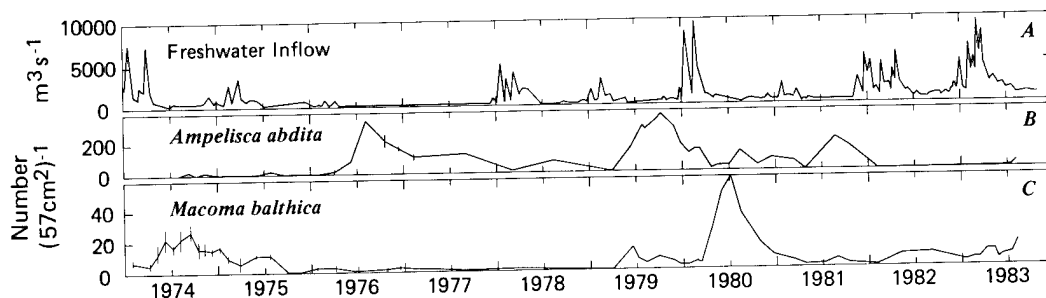


Figure 26. Average daily flow of freshwater into San Francisco Bay from the Sacramento and San Joaquin Rivers (A) and abundance of two species at the Palo Alto intertidal mudflat study site (B, C; from Nichols and Thompson 1985b).

of the mudflat at the mouths of local streams. It is not clear, in any instance, whether observed declines are related more to rapid sedimentation, to reduced salinity, or to some other related factor(s).

Episodes of unusually strong surface sediment erosion can also affect abundance by subjecting the small surface-dwelling invertebrates to physical removal or burial. As an extreme example, approximately 8 cm of sediment was removed from a South Bay mudflat between observations separated by one month during fall 1974 (Nichols and Thompson 1985a). The occasional accumulation and subsequent decomposition of macroalgal mats can also affect the benthic community. Again as an extreme example, a thick accumulation of the macroalga *Polysiphonia* covered the upper intertidal zone of a South Bay study site during summer of 1975, smothering the organisms in the sediments. Recolonization of the site required weeks to years, depending on the availability and motility of colonizing individuals, and seemed to involve migrating adults as well as juveniles (Nichols and Thompson 1985a).

3.2.2 Importance of Benthic Species Interactions

Other aperiodic changes may be manifestations of species interactions. Some species common to the bay benthic community, such as the clams *Macoma balthica* and *Mya arenaria* and the polychaete *Capitella*, display abundance patterns that are markedly discontinuous with time (Figure 21). *Capitella* (commonly called *C. capitata*, but actually comprising an

unknown number of sibling species; Grassle and Grassle 1976; hereafter referred to as *Capitella* spp.) appeared about 6 months after the macroalgal accumulation-and-decay event described above, but before the normally resident species had become fully reestablished. The *Capitella* group contains species that are well known exploiters of organically enriched or otherwise disturbed environments (Grassle and Grassle 1974, 1976; Nichols and Thompson 1985a). The availability of decaying organic matter, coupled with an absence of competitors, may have contributed to its temporary success.

Most other occasional species irruptions, such as that of *Mya arenaria* in 1975 (Figure 21), are not understood, although some explanations can be hypothesized. Several data sets, for example, show that *Macoma balthica*, sometimes absent for several years at a time, becomes abundant only when its larvae can settle in the relative absence of the introduced amphipod *Ampelisca abdita* (Figure 26). This finding suggests that *Macoma* abundance may be controlled locally by the presence of a large population of *Ampelisca* either by direct consumption of settling clam larvae or the physical disruption of larval settlement (Nichols and Thompson 1985a).

3.3 LONG-TERM TRENDS

The most pronounced change that has affected the benthic community of San Francisco Bay during the past 140 years was the introduction of species (Section 2.3). However, because quantitative studies of the benthos were not undertaken

until the 1950's, well after the period of most introductions, it is not possible to compare pre- and post-introduction benthic communities.

There is no indication from published reports that there have been significant long-term changes in benthic community composition during the three decades since quantitative studies began, although such changes have undoubtedly occurred in the immediate vicinity of waste outfalls (as a result of changed salinity regime as well as the effect of the waste flow itself;

Chapter 5). The absence of observable long-term changes at all other locations may be due, in part, to inconsistencies among the surveys in sampling location and time of year, sampling methodology, species identification, data interpretation, and discontinuous sampling through time within embayments (Nichols 1973). Qualitatively, the same common species names appear in all published species lists for each area. Only consistent, long-term, bay-wide monitoring will allow us to detect the existence or lack of significant trends.

CHAPTER 4. CYCLING OF MATTER IN THE BENTHOS

4.1 INTRODUCTION

Benthic biological processes are involved in the production, supply, transformation, and mineralization of organic matter in estuaries. To evaluate the biological productivity of the benthic community and its relation to fishery yield, for example, we must have knowledge of many processes that determine the fate of organic matter as it cycles through the ecosystem. Reproduction, recruitment, growth, and mortality in benthic macrofaunal populations (Chapter 3) are but a few of many biological processes that contribute to biogeochemical cycles. Primary production, aerobic and anaerobic respiration, chemosynthesis (= chemoautotrophy), and fermentation -- processes associated with algae, bacteria, fungi, protozoans, and meiofauna -- also contribute to the turnover of organic matter in sediments. Other processes including sedimentation, grazing, filter feeding, deposit feeding, predation of benthic invertebrates by fish and migratory birds, aerobic and anaerobic mineralization of all kinds of organic matter, and transport of resuspended material all contribute to the cycling of organic matter between the sediment and water column. In this chapter we consider some of the processes that govern the cycling of matter in the benthos.

4.2 SOURCES OF ORGANIC MATTER

The major sources of organic matter to the benthos are presumed to be the same as to the estuary itself: (1) plant material (algae and vascular plants) produced within the estuary, (2) living plant material and dead particulate material (detritus) suspended in the river

water and surface runoff that flow into the estuary, (3) dissolved organic matter from all sources, and (4) sewage from waste-treatment plants.

4.2.1 Vascular Plants

The marshes of San Francisco Bay and Delta, because of their greatly reduced size following more than 130 years of reclamation, are probably only a minor source of organic matter for the nonmarsh benthos of the bay. Atwater et al. (1979) estimated that production of dry vascular plant material in the bay's tidal marshes is about 1×10^5 tons per year. However, the amount of organic matter washed into the bay from those marshes may be only about 5% of the amount produced by phytoplankton in bay water (Atwater et al. 1979).

Eelgrass, Zostera marina, is also found in San Francisco Bay, but is apparently limited to the Central Bay region where salinity is highest (U.S. Fish and Wildlife Service and California Department of Fish and Game 1979). Eelgrass beds worldwide form complex habitats for associated fauna and flora and influence the benthic community by stabilizing sediment, providing substrate for epiphytes, producing organic matter, exporting detritus, and attracting predators such as crabs, shrimp, and skates (e.g., Phillips 1984). The disappearance of eelgrass from an area leads to extensive changes in sediment grain size, water chemistry, circulation patterns and turbulence, and species composition (Thayer et al. 1984). Nonetheless, scientific study of San Francisco Bay eelgrass beds has been minimal since the early studies by Setchell (1929). Other than aerial observations of

their distribution (U.S. Fish and Wildlife Service and California Department of Fish and Game 1979), little is known about the size of individual beds, total standing stock, seasonal and long-term fluctuations, eelgrass bed fauna, and the quantitative contribution of eelgrass to the organic matter budget of the estuary. Recently, however, an eelgrass transplant project used in mitigation for the loss of a bed during a U.S. Army Corps of Engineers seawall repair project (Fredette unpubl.) has stimulated renewed interest in bay eelgrass beds both with respect to mapping their distribution and studying their ecology (S. Wyllie Echeverria, California State University at San Francisco; pers. comm.).

4.2.2 Benthic Macroalgae

There are, at present, 162 species of macroalgae known to exist in San Francisco Bay (Josselyn and West 1985). The most widely distributed species are the green algae Enteromorpha clathrata, E. intestinalis, E. linza, Ulva angusta, Ulva lactuca, Cladophora sericea, and two red algae, Polysiphonia denudata and Antithamnion kyllini. Macroalgae are most commonly found growing in hard bottom areas (rock outcrops, coarse sediments, and human-made structures) in the central and northern regions of the estuary (Josselyn and West 1985). In summer, drifting macroalgae (detached from growing surfaces) occasionally accumulate in thick mats in the intertidal zone (Nichols 1979; Josselyn and West 1985). Their occurrence is generally viewed, because of their smelly decay, as a public nuisance rather than as important production of organic matter. Consequently, the main thrust of research has been dictated by the desire to control nuisance blooms that occur in some years (Josselyn 1984; Josselyn and West 1985). We do not know what triggers these localized, episodic blooms of drift macroalgae, nor do we know how much is produced in situ and how much accumulates by physical transport and mixing processes.

Macroalgae are recognized as an important source of the bay's organic matter, but their total contribution to benthic primary production has not been assessed. Thus, the importance of macroalgae as a source of food for benthic

organisms of the bay is also little understood. The largely descriptive (Silva 1979; Josselyn and West 1985) and physiological (Shellem and Josselyn 1982) studies of the bay's macroalgae need to be supplemented by field measurements to obtain the necessary spatial and temporal estimates of natural production.

4.2.3 Phytoplankton

Phytoplankton abundances in the bay are controlled largely by light availability and vertical mixing processes that result in a spring bloom in South Bay and a summer bloom in Suisun Bay (Figure 27). Annual net production of phytoplankton in the photic zone varies from 95 to 150 g C/m² and is highest in South Bay where turbidity is lowest, although biomass is highest in the entrapment or null zone of Suisun Bay (Cloern et al. 1983; Cole and Cloern 1984). Results from several studies (Cloern 1982; Hammond et al. 1985) suggest that much of the phytoplankton produced in the water column settles to the bottom, where it is consumed by a variety of organisms from bacteria to large clams and worms.

Light and nutrients (from the rivers, waste-treatment plants, and within-estuary remineralization) are sufficient to support much larger blooms of phytoplankton than are typically observed. Therefore, we might expect the occurrence of nuisance blooms of algae that could deplete the oxygen supply in the water and kill planktonic and benthic animals. The lack of such nuisance blooms in San Francisco Bay has been attributed, at least in part, to benthic grazing (Section 2.5.1; Cloern 1982; Nichols et al. 1986).

The coastal ocean is also a source of nutrients for San Francisco Bay, particularly during the summer upwelling season (Conomos et al. 1985). But, to what degree the coastal ocean is a source of plankton-derived organic matter is unknown, although neritic (coastal ocean) diatoms are common in the central part of the bay (Cloern et al. 1985). Wolff (1977) showed that organic detritus from the coastal sea was an important source of food for the benthos of the Grevelingen Estuary (The Netherlands) before it was converted to a lake.

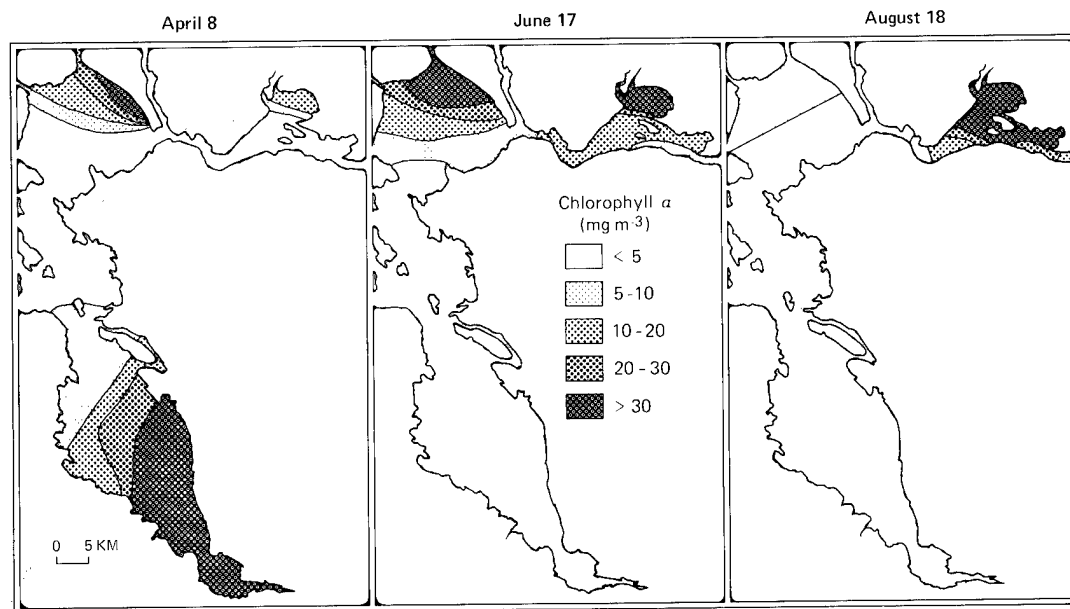


Figure 27. Contours of near-surface phytoplankton biomass (measured as chlorophyll) in San Francisco Bay on three occasions in 1980 (from Cloern et al. 1985).

4.2.4 Benthic Bacteria and Microalgae

The primary producers on estuarine sediments (excluding marshes, macroalgae, and seagrass beds) are photosynthetic bacteria, diatoms, and bluegreen algae (cyanobacteria). Photosynthetic bacteria, which produce sulfur rather than the easily measured oxygen, occur under conditions of anoxia either in sediment or in water, where both hydrogen sulfide and light are present. These bacteria can be a major primary producer in stratified briny lakes and ponds which, because they do not mix vertically, become anoxic at some depth within the photic zone (Fenchel and Blackburn 1979). Carpelan (1957) noted the presence of sulfur bacteria in South Bay salt-evaporating ponds. However, because the water in the salt ponds is not discharged into the bay, these bacteria are probably not a significant source of organic matter for the bay.

Little quantitative information is available about the contribution of microalgae (diatoms) to the organic matter budget of the bay benthos. Recent studies suggest, nonetheless, that benthic diatoms growing on the sediment surface throughout

the bay, together with temporarily or permanently settled phytoplankton, may represent the most readily available food resource for bottom organisms in this shallow estuary (Nichols and Thompson 1985a; see also Christensen and Kannevorf 1985 for a pertinent study elsewhere). A 1-year survey of the distribution of benthic chlorophyll in bay sediments showed highest levels of microalgal biomass (up to 300 mg/m^2 chlorophyll *a* at some stations) in the southernmost and northernmost ends of the bay, and the lowest levels (20 mg/m^2) both in San Pablo Bay (Figure 28) and in the deeper channels. Limited by light availability, chlorophyll reaches higher concentrations in intertidal and shallow subtidal (less than 5 m deep) sediments than in deep water sediments (e.g., 170 mg/m^2 versus 50 mg/m^2 in Suisun Bay; Thompson et al. 1981).

Seasonal patterns in benthic plant biomass varied from embayment to embayment depending on light levels which are controlled by the turbidity of inflowing freshwater and the tide- and wind-induced resuspension of surficial sediments (Nichols and Thompson 1985b). For example, maximum biomass in South Bay was found in spring, approximately coincident with the phytoplankton bloom. The timing

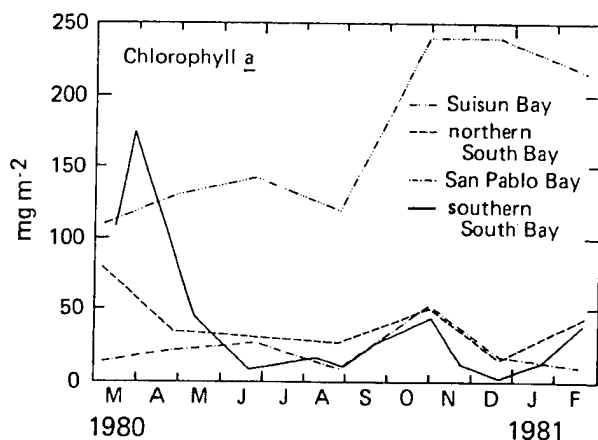


Figure 28. Average chlorophyll concentration in surface sediments at sites less than 5-m water depth; data from same stations as sediment data shown in Figure 10.

of the bloom coincided with the annual peak in solar radiation at low tide. Increased suspended sediment concentrations, coincident with peak wind velocities in May and June and peak tidal velocities in June and July at the time of maximum solar irradiance (Figure 29), may limit benthic microalgal biomass during late spring and summer.

Maximum benthic chlorophyll biomass in Suisun Bay was not observed until late October. The Suisun Bay benthic diatom bloom consisted primarily of *Thalassiosira decipiens* (R. Laws, Univ. North Carolina; pers. comm.), the same species responsible for the major phytoplankton bloom in Suisun Bay during the previous month (Cloern et al. 1985). This species has high sinking rates (1.5 to 6 m per day; Ball and Arthur 1981) and apparently resides alternately in the water column and in sediments depending on the degree of water-column mixing (Cloern et al. 1985; Nichols and Thompson 1985b). The diatom cells apparently settle to the bottom following the autumn plankton bloom during a period of low river inflow and reduced tidal current and wind velocities (Figure 29a,b; Nichols and Thompson 1985a).

Elsewhere in the bay, the species composition of benthic diatom communities varied with salinity and water depth (Laws 1983, pers. comm.). Species diversity increased with increasing salinity toward

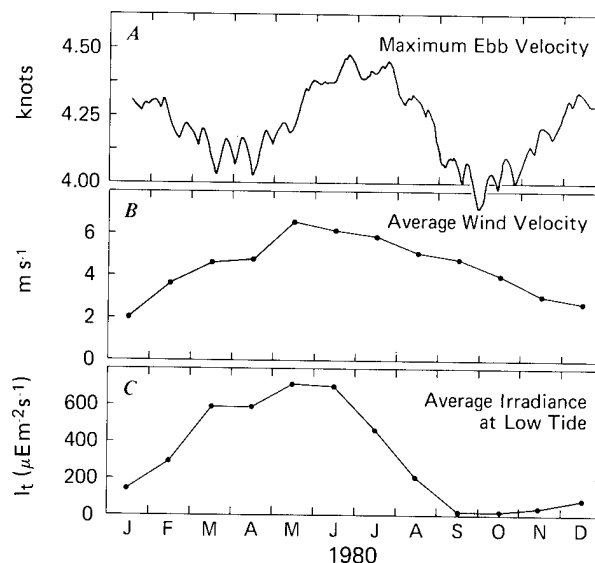


Figure 29. (A) Daily maximum ebb tidal velocity at the Golden Gate, (B) average monthly wind velocity at San Francisco International Airport located just south of the city of San Francisco, and (C) average monthly instantaneous irradiance at the time of low tide (from Nichols and Thompson 1985b).

the deeper water of Central and South Bays, where species tolerant of higher salinity (e.g., *Paralia sulcata* and *Ditylum brightwellii*) were found (Laws 1983). The highest diversity among benthic diatom communities in San Francisco Bay was found in the sediments of the shallow margins of South Bay where there is no major freshwater source. This assemblage was dominated by estuarine benthic species (e.g., *Nitzschia acuminata* and *N. pusilla*). Preliminary analysis of species distributions over one year showed that species composition changes seasonally, partly because seasonally varying winds and tides resuspend and mix sedimentary material, and thus influence the mix of benthic and planktonic forms found in the benthic diatom assemblage (Laws, unpubl.).

4.2.5 Microalgal Production

Existing measurements of chlorophyll concentration in surface sediments have not been accompanied by systematic measurements of benthic primary production, despite the results from many

studies worldwide (reviewed by Parsons et al. 1984) that demonstrate the importance of such measurements to an understanding of net community production. The progressive buildup of diatom mats on intertidal flats of San Francisco Bay during late winter and early spring is evidence of its potential importance here as well.

Because of the shallowness and periodic inflow and outflow of water, plankton production over an intertidal zone may be small relative to benthic production under both clear water (Pamatmat 1968) and turbid water (Hargrave et al. 1983). Furthermore, since the phytoplankton present in the water column can consist, in part, of benthic diatoms that are resuspended by waves and tidal currents, the distinction between planktonic and benthic primary production in a shallow estuary can be an artificial one.

To properly assess the relative importance of phytoplankton and benthic microalgae in San Francisco Bay, where the photic zone extends to the bottom in a large but unknown fraction of the total area, the measurements of primary productivity will have to be conducted from the intertidal zone to the midbay channels within each embayment. Understanding the quantitative relation between natural light and benthic primary production in San Francisco Bay, where waves and tidal currents repeatedly blur the boundary between benthos and water column, will be critical to such investigations. One broad question concerns the effects of wind-generated sediment resuspension (a daily occurrence in the summer) on photosynthetic rates on the bottom as well as in the water column. Light transparency and the amount of light reaching the bottom are reduced during periods of resuspension, tending to diminish benthic production. The loss of production on the bottom may, however, be compensated by the enhanced growth of "benthic" diatoms while they are suspended in the water column. If the diatoms grow at least as fast in suspension as on the bottom, and then settle to the bottom during slack tides or windless periods, organic matter supply to the bottom is not impaired by sediment resuspension and turbidity. Even so, the relative importance of the benthos and the plankton as grazers would have to be evaluated.

4.2.6 Other Sources of Organic Matter to the Benthos

Other sources of organic matter that are potentially important to the benthos, but that are poorly studied to date, include dissolved organic matter and detritus. The input rates and character of dissolved organic matter entering the bay are unknown. And, other than qualitative descriptions of river-borne detritus (e.g., Knight et al. 1980), information about the amounts and role of detritus (and its associated microbial community) is also very limited. Further, no measurements of the supply of particulate organics to the bottom, nor estimates of the relative importance of the two major sources of organic materials (internal and external) have been made.

4.3 RATE OF ORGANIC MATTER SUPPLY

Below the photic zone, the benthos is dependent on the supply of organic matter from above, including settling plankton and its remains, detritus transported in rivers, surface runoff, sewage treatment plant effluents, and detritus mobilized by storm waves and shore erosion from surrounding marshes and tideflats, and carried by tidal currents to the open bay. The metabolic rate, energy flow, and productivity of the benthic community, and ultimately its capacity to sustain a fishery, depends upon the rate at which this organic matter is supplied (Hargrave 1973; Pamatmat 1977). Needless to say, the rate of supply of organic matter to the benthos of San Francisco Bay is unknown.

While there may be interest in measuring the rate of organic matter supply to the benthos, it cannot be measured directly with existing methods (passive collectors in the water column or on the bottom) because of the predominance of resuspension and horizontal advective transport processes associated with river discharge and tidal currents. Furthermore, filter feeders such as clams and mussels apparently actively remove large quantities of phytoplankton from within the water column. That is, they are not necessarily passive collectors of settled particles.

A combination of independent measures may be useful in estimating total

benthic supply (i.e., summing the losses of organic matter from the bottom -- benthic metabolic oxidation, burial rate, and rate of predation on benthos by demersal fish, plus loss of organic matter with sediments leaving San Francisco Bay). Meanwhile, we can only guess at answers to questions that involve the amount and fate of organic matter entering the bay, such as (1) the total biological productivity of the benthos, (2) the capacity of the bay organisms to decompose organic waste from domestic sewage effluents, and (3) whether the benthic community's functions have been impaired by pollution.

4.4 FATE OF ORGANIC MATTER IN SEDIMENTS

Benthic energy flow and biogeochemical cycles are linked to the fate of organic deposits in the bottom. Part of the settling organic matter is ingested directly by macrofauna, digested, and metabolized to carbon dioxide, water, and dissolved nutrients such as nitrates and phosphates. The uneaten and undigested fraction enters the detrital food web (Fenchel and Jorgensen 1977) where complex organic matter is further transformed and mineralized by a variety of metabolic types of microorganisms.

Complex organic substances degrade as they pass through the metabolic web (Figure 30). While breaking down complex molecules, microbes synthesize proteins, polysaccharides, nucleic acids, and other matter whose complexity is equal to or greater than that of their substrate. The microbes are ingested, digested, and metabolized by selective and nonselective deposit feeders (meiofauna and macrofauna). Microbes and higher forms of organisms are similar in metabolizing part of their food into smaller molecules or the mineral building blocks of organic matter, and resynthesizing part into complex molecules that make up their respective biomass. Since decomposition is the breakdown of dead organic matter, it is not a microbial process alone. The "decomposer" compartment in ecosystem models has no distinct functional reality like primary producer, chemoautotroph, sulfate reducer, etc. The benthic community as a whole is a decomposer and mineralizer of the organic matter available in the system.

The natural rates of benthic microbial processes in San Francisco Bay, which must be known for quantitative modeling of the sediment organic matter budget, have not been measured. Instead,

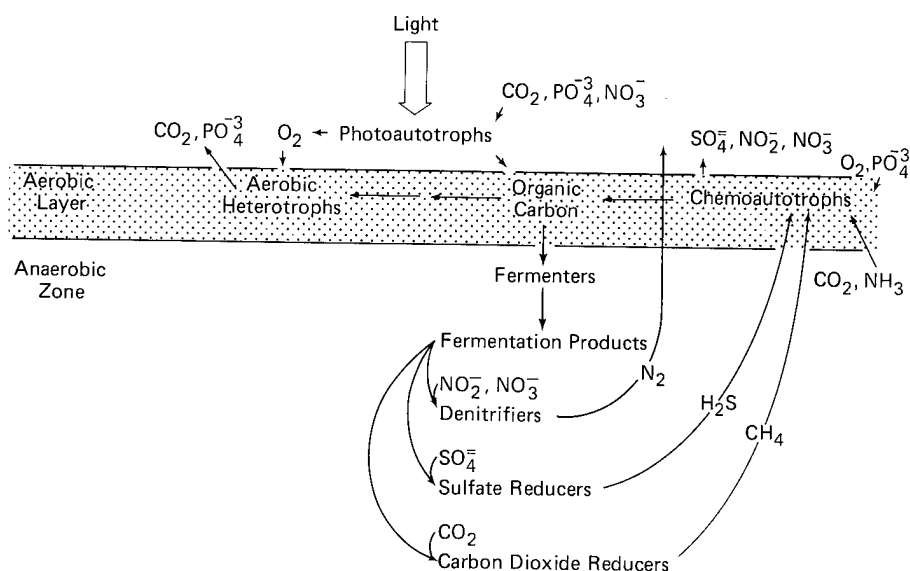


Figure 30. Relations among aerobic processes in the oxic surface sediment layer and anaerobic processes in the deeper anoxic layers. Acid fermentation produces organic acids, hydrogen, and carbon dioxide, which are utilized in different anaerobic respiratory processes, producing reduced inorganic substances that are oxidized by chemoautotrophs.

work on San Francisco Bay sediment microbiology has been focused on denitrifiers (Oremland et al. 1984; Miller et al. 1986), sulfate reducers (Oremland and Silverman 1979), and methanogens (Oremland 1981; Oremland and Polcin 1982; Oremland et al. 1982), with the following objectives: (1) to examine the biogenic origin of hydrocarbon gases in sediments (Oremland 1981; Vogel et al. 1982); (2) to clarify the interactions between sulfate reducers and methanogens (Oremland and Polcin 1982; Oremland et al. 1982); (3) to show the anaerobic degradation of specific organic compounds (Smith and Oremland 1983); (4) to explain the occurrence of methane in surface waters (Oremland 1979); and (5) to identify the anaerobe's natural energy and carbon sources (Oremland and Silverman 1979). These studies demonstrate the involvement of anaerobes in various chemical transformations in the bay and give us some of the necessary knowledge for accurate modeling of sediment processes. For example, some methanogenic bacteria produce ethane, methane, ethene, propene, propane, and butane (Oremland 1981; Vogel et al. 1982). Because these gases can bubble out of the sediments (Oremland and Silverman 1979), their losses must be accounted for in an accurate carbon budget.

4.5 SEDIMENT OXYGEN CONSUMPTION

The oxygen uptake by sediments has commonly been measured because of its perceived equivalence to benthic community metabolism and energy flow (Teal and Kanwisher 1961). The rate of oxygen uptake has been found to be related to the rate of organic matter supply, temperature, hydrostatic pressure, pH, tidal cycle, diel cycle, oxygen tension, organic pollution, organic matter content of sediments, bacterial count, and macrofaunal irrigation of tubes and burrows. Some of these factors are obviously interrelated (Pamatmat 1977). The particular dependence of benthic oxygen consumption on phytoplankton production and subsequent sedimentation of organic matter to the bottom is now clear (Hargrave 1973).

The only published data for San Francisco Bay (Hammond et al. 1985) come from two sites in South Bay (Table 4). Rates of oxygen consumption and carbon dioxide production were higher at a shallow site (1.5-m water depth) than at a deeper site (14-m depth). These results suggest a higher rate of organic matter deposition at the shallow site. Overall, the rates fluctuated seasonally by a factor of 1.5 around an average of 27 mmol

Table 4. Rates of benthic oxygen uptake and carbon dioxide production in South Bay (Hammond et al. 1985).

| Date | T °C | mmol O ₂ /m ² /d (± std. error) | mmol CO ₂ /m ² /d (± std. error) | RQ(=CO ₂ /O ₂) |
|-----------------------|------|--|---|---------------------------------------|
| Shallow station (1.5) | | | | |
| Feb 1980 | 12 | 13 | Not measured | |
| Jun | 17 | 46 ± 9 | 43 | 0.9 |
| Nov | 16 | 28 ± 6 | 16 ± 3 | 0.6 |
| Feb 1980 | 12 | 17 ± 5 | 14 ± 5 | 0.8 |
| Annual average | | 30 ± 7 | 24 ± 8 | |
| Deep station (14 m) | | | | |
| Feb 1980 | 12 | 16 ± 11 | Not measured | |
| Jun | 17 | 22 ± 8 | 33 ± 1 | 1.5 |
| Nov | 17 | 11 ± 2 | 16 ± 5 | 1.5 |
| Feb 1981 | 12 | 11 ± 2 | 10 ± 5 | 0.9 |
| Annual average | | 16 ± 7 | 20 ± 4 | |

/m²/d, but the 1.5-m-deep location showed a greater seasonal amplitude than the 14-m site. The rates ranged from 11 mmol/m²/d in the fall/winter at 14 m to 46 mmol/m²/d in the summer at 1.5 m. These values are in the low to middle part of the range (14 to 95 mmol/m²/d) observed in a variety of coastal marine systems (Nixon 1981).

The ratio of moles CO₂ produced to moles O₂ consumed, known as the respiratory quotient (RQ) in animal metabolism, is a useful indicator of metabolic activity. The aerobic oxidation of fats, proteins, and carbohydrates results in a value of 0.7, 0.85, and 1.0, respectively. Thus a range of 0.7 to 1.0 suggests that organic matter of mixed composition is essentially mineralized by aerobic respiration. Values of RQ greater than 1 arise when anaerobic respiration (denitrification, sulfate reduction, etc.) produces CO₂ in addition to that which is produced by aerobic respiration at the sediment surface. A value less than 0.7 signifies the uptake of oxygen by inorganic chemical oxidation reactions without a corresponding production of CO₂, e.g., sulfide oxidation and ferrous-iron oxidation. The foregoing interpretation does not take into account the role of chemoautotrophs, which utilize both oxygen and carbon dioxide to produce organic matter (Pamatmat 1986). The ratio has been used as an indication of aerobic-anaerobic balance in benthic systems (Pamatmat 1984, 1986). Hammond et al. (1985) obtained values between 0.6 and 1.5 at their two sites in South Bay. The ratios at their shallow site were less than 1.0, while the 14-m depth showed a range of 0.9 to 1.5.

Hammond et al. (1985) compared the annual sediment oxygen uptake, or its carbon equivalent, with the estimated annual phytoplankton production and concluded that benthic biological processes altogether remineralize 70% to 90% of particulate organic carbon produced by phytoplankton. These data support the observation that grazing by benthic invertebrates is a primary mechanism controlling phytoplankton blooms in South Bay (Cloern 1982). The oxygen-uptake, phytoplankton-production comparison does not include the contribution of benthic primary production plus other forms of organic matter that enter the South Bay from surface runoff, streams, effluents from sewage treatment plants, and detritus from surrounding marshes. It is important

therefore to have an independent and possibly direct measure of organic matter sedimentation to the bottom. However, because studies to provide direct measurements of organic matter supply to the benthos of San Francisco Bay have not been undertaken, we must find other ways to complete the benthic budget of organic matter and improve our estimates of metabolic losses in the sediment.

4.6 BENTHIC NUTRIENT REGENERATION IN SAN FRANCISCO BAY

The biological productivity of San Francisco Bay, as elsewhere (see Zeitzschel 1980), is controlled in part by the interactions between the benthos and the water column. As water depth increases, benthic mineralization decreases and metabolic oxidation by the plankton increases, primarily because of the longer residence time of organic particles in the water column (Hargrave 1973). In shallow estuaries such as San Francisco Bay, however, the benthos plays a dominant role. The controlling influence by the benthos can be measured in terms of (1) its rate of removal of organic matter from the water column, (2) its rate of degradation of settled organic matter, and (3) its rate of release of primary nutrients to the overlying water.

Hammond et al. (1985) used in situ flux chambers at two stations to measure changes in concentrations of radon, oxygen, ammonia, carbon dioxide, silica, alkalinity, nitrate plus nitrite, and phosphate in the enclosed water (e.g., Table 4). Pore-water profiles of nutrients and radon were also determined. Calculations of benthic fluxes from the profiles were consistent with chamber measurements and indicated that O₂, CO₂ and nitrate-nitrite fluxes were the result of reactions occurring in the top few centimeters of sediment, while the fluxes of NH₃, SiO₂, and alkalinity were driven by reactions proceeding in the entire 20- to 40-cm sediment column. Seasonal and spatial differences in fluxes showed the effects of temperature, spring phytoplankton bloom, and the irrigation of burrows through respiratory activity or locomotion of infauna. The fluxes of these dissolved materials in South Bay were similar to those measured in other temperate estuaries with the same level of primary production. Smaller seasonal

amplitudes in San Francisco Bay were attributed to the relatively small seasonal temperature range.

Mass balance calculations for South Bay (Hammond et al. 1985) indicated that about 65% of silica in the annual phytoplankton primary production was recycled by the benthos. The silica flux could replenish the standing stock in the water column in 17-34 days. Also, benthic nitrification and denitrification were shown to convert 55% of organic nitrogen reaching the sediments into nitrogen gas. Ammonia flux could replace standing stocks in the water column in 2 - 6 days. All of these figures demonstrate the quantitative importance of the benthos in the biogeochemical cycle of the estuary.

4.7 MODELS OF ORGANIC MATTER BUDGETS OF ESTUARINE BENTHOS

Our present comparisons of estuaries are limited by too few known quantitative relations. Hargrave's (1973) empirical equation relating benthic oxygen uptake to plankton primary production and mixed layer depth,

$$\text{sediment } O_2 \text{ uptake (l/m}^2\text{/yr)} = a(C/Z_m)^b,$$

where a and b are constants, C is net annual primary production in $g\ C/m^2$, and Z is mixed-layer depth (the thickness of the vertically mixed water layer), is a step towards quantitative modeling of benthic activity. For an estuary with diverse sources of organic carbon, however, Hargrave's model of benthic oxygen consumption ignores many factors related to total energy supply. For example, predation is believed to be a significant factor in Chesapeake Bay (Kemp and Boynton 1981) and may be in San Francisco Bay as well. A model incorporating all such factors is important.

A model combining all known factors and properties and describing how they quantitatively determine the ecology of the benthos and San Francisco Bay as a whole would be a valuable management tool. Kremer and Nixon (1978) have set an example for simulating the properties and processes occurring in an estuary.

The sum of all the organic matter coming from the various sources discussed above, plus the amounts discharged by

municipal sewage-treatment plants and carried by surface runoff directly into the bay, make up the total input to the bay. From this, the total amount metabolized in the water column and exported to the open ocean must be subtracted to obtain an estimate of the amount that settles to the bottom. The organic matter that reaches the bottom is dissipated by benthic metabolism, removed and exported by predation and sediment erosion, and removed from the biogeochemical cycle by burial.

A summary of the known sources and sinks of organic matter follows.

Total bay input = Plankton primary production

- + Macroalgal primary production
- + Benthic microalgal primary production
- + Eelgrass production
- + River-borne detritus
- + Marsh-derived detritus
- + Sewage-derived detritus
- + Surface-runoff-derived detritus
- + Dissolved organic matter from all sources
- + Matter entering the bay from the ocean

Benthic supply = total bay input

- Plankton metabolism
- Export to the ocean

At steady state, Benthic supply = Benthic losses.

Benthic losses = Metabolic oxidation by community

- + Removal by migratory demersal predators
- + Export via erosion of sediment

- + Removal by burial
- + Loss of gametes and larvae
- + Loss of dissolved substances

Many terms of the organic matter budget of the bay are unknown, including the character and rates of organic matter input to the benthos. Even in a study of an estuarine system for which much more detailed data on the partitioning of organic matter are available (e.g., Marshall 1970), it is still an exceedingly difficult task to translate those data into an understanding of, for example, the absolute yield of commercially exploitable species. Better knowledge about the

dynamic relation among the separate components of the estuary (benthic versus pelagic, living versus nonliving) is essential if we are to answer a broad range of questions related to fisheries production, effects of pollution, capacity of the bay to decompose organic wastes, and occurrence of nuisance blooms of macroalgae. For the present, we have only separate pieces of comparative information from different estuaries. The existence of data from other ecosystems and knowledge of general principles derived elsewhere, while helping us design research plans for future studies of the bay, do not provide the kind of specific detail we need to predict important ecosystem responses in San Francisco Bay.

CHAPTER 5. ANTHROPOGENIC INFLUENCES

The San Francisco Bay Estuary and its drainage basin, like many estuarine systems throughout the world, have been affected by human activity (Nichols et al. 1986). The bay area has been populated by American Indians since at least the end of the last glacial period, although most remains of bay-area inhabitants prior to 5,000 years ago have presumably been covered by the sea (Atwater 1979). Until the arrival of European colonizers, an estimated 20,000 to 25,000 Indians lived in several hundred small villages and depended on the bay for a large proportion of their food (Bolton 1927; U.S. Fish and Wildlife Service and California Department of Fish and Game 1979).

Spanish soldiers and missionaries, first discovering the bay in 1769, found a vast complex of open-water bays and surrounding fresh- and saltwater marshes with plentiful game animals, birds, and fish. The tidal marshes alone covered an estimated area of about 2,200 km² (Gilbert 1917). This landscape changed as the culture changed, but particularly after the discovery of gold in 1848 when California was inundated with immigrants. Now, all that remains of the aboriginal culture, which had changed little with the passage of millenia, are a few of the more than 400 shell middens (the debris of the aboriginal diet consisting largely of shellfish) that were mapped about 1900 (Nelson 1909, 1910) (Figure 31). The rest of the middens have long been buried or eliminated by urban and industrial development. Similarly, the estuary has been changed by land reclamation, over-fishing, and waste discharge within the estuary; agricultural practices in the Central Valley (Federal Water Pollution Control Administration 1967); hydraulic gold mining in the mountains (Gilbert 1917); and management of river flow (Nichols et al. 1986).

Human influence on the bay ecosystem is seen most clearly as change in the composition of the biotic community, reduction or elimination of some of the bay's natural resources, and deterioration in the aesthetic and recreational value of

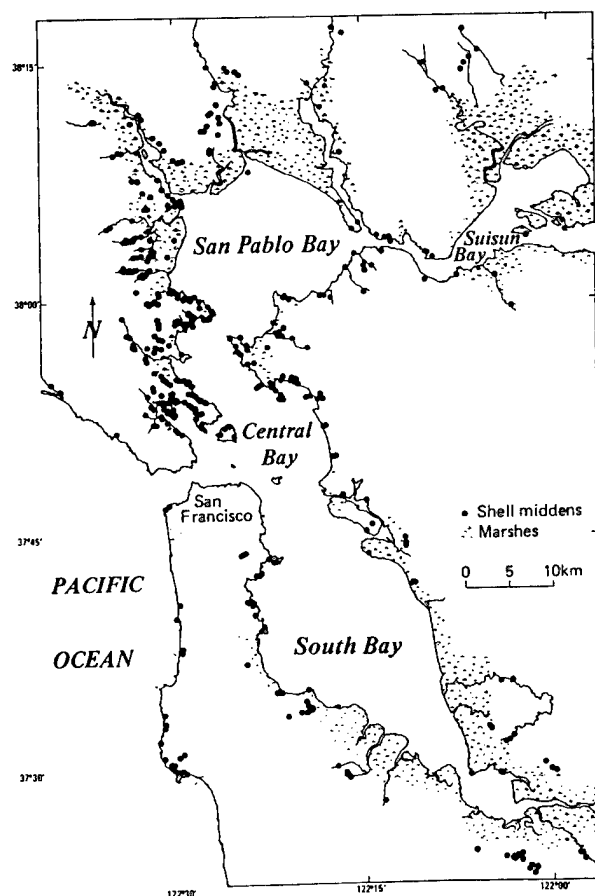


Figure 31. Distribution of Indian shell middens and tidal marshes at about 1900. Most middens are now covered by urban development (map adapted from Nelson 1909).

the estuary. The potential agents for unwanted change are physical alteration of the bay's shoreline and bathymetry, over-exploitation of its resources, interference with the natural hydrologic cycle, and disposal of human and industrial wastes and dredge spoils.

5.1 EARLY PHYSICAL AND BIOLOGICAL CHANGES

Rapid sedimentation of gold mining debris caused unintentional shoaling of the bay and its tributary streams and rivers during the period of hydraulic mining in the Sierra Nevada Mountains between 1851 and 1884. At its maximum use, hydraulic mining turned over tens of millions of cubic meters of gold-bearing material annually (Gilbert 1917). The mining residue, consisting of mud, sand, gravel, cobbles, and boulders, washed from the hillsides and choked the creeks and rivers of the Sacramento and San Joaquin Rivers. During succeeding decades, much of the mud and sand was flushed out of the rivers and into San Francisco Bay (Gilbert 1917; Atwater et al. 1979). By the end of the 19th century, 1.0, 0.75, and 0.25 m of sediment had been deposited in Suisun, San Pablo, and Central Bays, respectively, creating large shoal areas, reducing the water volume of the bays, and altering circulation patterns (Gilbert 1917).

The shoreline of the bay was also greatly altered. The area of the marshes prior to 1850 was estimated at about 2,200 km² (Gilbert 1917). Leveeing and filling of the bay perimeter to create agricultural, commercial, industrial and residential land reduced the area of the unleveed tidal marshes by about 95% (Atwater et al. 1979; Josselyn 1983). Some of the leveed regions (primarily agricultural land adjacent to Suisun and San Pablo Bays and in the Delta, and salt evaporation ponds in South Bay) retain some wetland characteristics ("seasonal wetlands"), and thus provide valuable habitat for aquatic birds.

The loss of tidal wetlands meant the elimination of much of the estuary's vascular plant primary production, a potential source of food for benthic organisms throughout the bay. The loss of wetlands has also meant loss of migratory shorebird habitat, and with it a loss in the number of waterfowl using the bay (Skinner 1962). However, quantifying any

change in the capacity of the bay to produce harvestable protein, long after the change occurred, is impossible. The only possible benefits to the benthos of San Francisco Bay resulting from the nearly complete modification of the shoreline are (1) the possible reduction in shorebird predation because of the presumed reduction in shorebird abundance (through hunting pressure and loss of habitat), and (2) the addition of new habitat for some of the introduced species such as the Japanese littleneck clam, Tapes philippinarum, through the construction of levees and seawalls (McAllister and Moore 1982).

Contamination of the bay by human and industrial wastes was recognized as early as 1900 (e.g., Nelson 1909; Skinner 1962). As late as the mid-1950's, levels of water-column oxygen concentration at or near 0 mg/l were common in South Bay during summer (Pearson 1958; Storrs et al. 1966), with the result that few or no animals were found in South Bay sloughs (Brown and Caldwell Engineers 1954).

The effects of the introduction of species on benthic community structure were marked: the new species are now clearly predominant in the community in both abundance and biomass (Section 2.3). We can only guess now at the nature of the ensuing interactions and changes in functional relations, overall biological productivity, and community energetics that occurred progressively as one introduced species after another became established.

5.2 INTERFERENCE WITH THE NATURAL HYDROLOGIC CYCLE

Seasonal patterns of river flow and total annual flow are major factors determining the bay's salinity distribution and patterns of circulation and mixing (Walters et al. 1985). The salinity of the bay fluctuates greatly from season to season in response to the winter high-flow and summer low-flow pattern (Section 1.3) and between years in response to year-to-year differences in rainfall and runoff (wet versus dry years). These fluctuations in salinity and in other physicochemical attributes of the bay result directly in marked temporal changes in all of the biological communities of the estuary (Cloern and Nichols 1985). In

winters and during wet years, most estuarine benthic species are restricted to the part of the bay west of Carquinez Strait because of their intolerance of freshwater. The degree of displacement depends on the magnitude and duration of the winter-spring freshet. In summer, when salinity increases, the estuarine species recolonize the previously vacated areas. Despite the typically large seasonal and interannual variations in species abundances and distributions, benthic community composition over the long term seems to have remained stable (Chapter 3).

Against the background of naturally varying river inflows, detection of the effects of freshwater impoundment (reducing the natural volume of river inflow) on the bay's benthos is difficult. This is the case because there are no long-term bay-wide data on species distributions and abundances that would allow us to uncover direct associations with river flow.

The occasion of the 1976-77 drought along the west coast of North America offered a "worst-case" example of the relation between reduced flows and balances among the aquatic communities of the bay. During the drought, inflow from the Sacramento-San Joaquin River system was greatly reduced and the typical summer phytoplankton maximum in Suisun Bay was absent despite greatly increased water clarity (reduced suspended sediment load). Perhaps as a consequence of the low phytoplankton biomass, zooplankton, shrimp, and larval striped bass in Suisun Bay were also found at very low levels. Cloern et al. (1983) suggested that the typical summer phytoplankton maximum during the period of extremely low summer flow (less than 100 m³/s) was moved upstream into the deeper Sacramento River where light limited growth. Simultaneously, benthic species normally restricted to the more saline waters west of Carquinez Strait migrated upstream into Suisun Bay and established dense populations (Nichols 1985b). These populations may have sufficiently grazed the phytoplankton to contribute to the declines of the pelagic consumers. From this scenario, one can conclude that during any prolonged period of reduced river flow, when Suisun Bay salinity remains above zero during winter, the dominant food web of Suisun Bay could

shift from pelagic to benthic and, as a result, affect the pelagic fishery yield there. In contrast, during spring of years with high river inflow, standing stocks of phytoplankton, at least in South Bay, are highest because the freshwater surface layer that penetrates into South Bay enhances water column stability that favors a larger phytoplankton bloom (Cloern et al. 1985).

The observed changes in the food web of northern San Francisco Bay under prolonged conditions of reduced river flow, while the result of an extreme natural event, are important in the context of proposals to increase rates of water diversion in the future (e.g., Meral 1982). The concern is that without some limits on the rate and timing of interruptions of the flow of freshwater to the bay, changes in plant and animal communities like those seen during the 1976-77 drought could occur during future dry periods. Such changes, if sustained, might affect fishery resources. While our present evidence for such a direct relation in San Francisco Bay is scanty, large declines in fish catches in many other estuaries have followed large-scale impoundments of freshwater (Rozengurt and Herz 1981).

Increased freshwater diversion may also influence the chemical contamination of the estuary. During the 1976-77 drought years, the bottom deposit of the lower Sacramento River changed from sand to mud, and increased in oil, grease, and metal content (Siegfried et al. 1980). There is evidence that the freshwater flows from the Sacramento and San Joaquin Rivers significantly affect the concentration of contaminants in sediments and organisms elsewhere in San Francisco Bay: the lowest concentrations of silver in clams collected from South Bay were observed during high-flow years (Figure 32). Although the mechanisms are not yet clear, contaminants are more rapidly assimilated by or flushed from the bay during periods of high river flow (Luoma et al. 1985). Further, decreased river inflow to the bay means that waste water becomes a larger percentage of the total flow of water into the bay (Russell et al. 1982).

Another typical consequence of reduced river inflow to estuaries is decreased sediment input and increased water transparency (Krone 1979). This

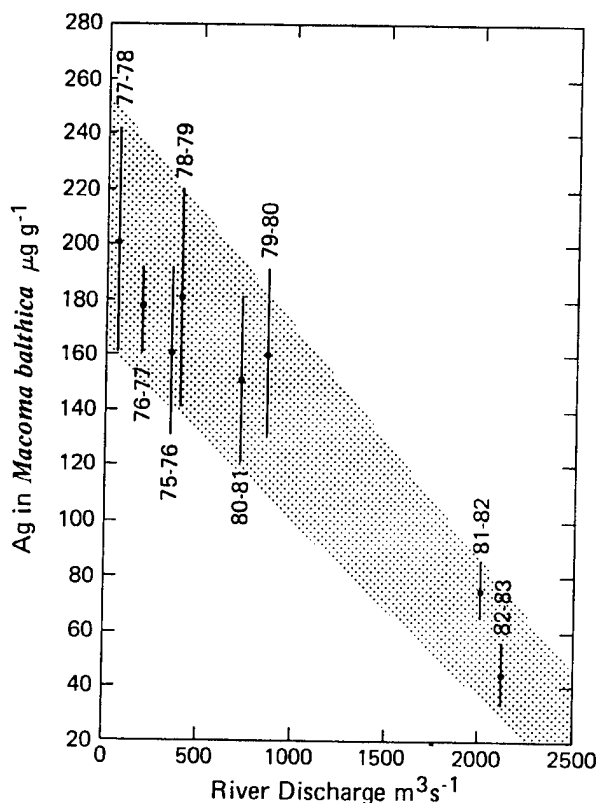


Figure 32. Relation between the winter maximum concentration of silver (average and 95% confidence limits) in *Macoma balthica* from the Palo Alto study site (Figure 4) and the rate of freshwater inflow from the Sacramento-San Joaquin River system during December (from Luoma et al. 1985; silver concentrations erroneously reported therein as milligrams per gram).

could be an important issue if, during periods of low river inflow, decreased turbidity favored nuisance blooms of algae. As mentioned above, however, phytoplankton declined during the 1976-77 drought period. Macroalgae, unaffected by benthic filter feeding, might be expected to proliferate as a result of increased water clarity. Curiously, however, no unusual macroalgal blooms occurred during the drought years. What is clear from this observation is that while we may know how individual estuarine properties (e.g., sediment load, salt balance, residence time, nutrient load) will change in response to changes in river inflow, we find it difficult to predict ecosystem-level consequences.

The long-term effect of further increases in freshwater diversion on benthos production is also unclear. An important test of our understanding will be to determine whether the same set of biological conditions observed in northern San Francisco Bay during the drought years (large benthic invertebrate biomass, reduced phytoplankton biomass), will recur during the next drought period. The theory raises other questions as well. If the benthos becomes more prominent in northern San Francisco Bay as a result of increased salinity, will a benthic food web replace the present planktonic food web and result in the decline of pelagic food species in that part of the estuary? Answers to this and related questions are, as yet, beyond our reach.

5.3 EFFECTS OF POLLUTION

Approximately 30 municipal and 40 industrial waste-treatment facilities and an additional 100 smaller industrial plants discharge treated waste into San Francisco Bay, while more than 50 small local streams discharge untreated waste from urban runoff. Additional waste, largely from agricultural regions, enters the bay in the flows from the Sacramento and San Joaquin Rivers (Nichols et al. 1986). The bay annually receives 5,500 tons of oil and grease and 438 tons of other pollutants (372 tons of which are heavy metals) from industrial and domestic sewage-treatment plants (Citizens for a Better Environment 1983). Although the data are extremely limited, the amounts of heavy metals from river inflows and surface runoff flowing untreated into the bay are estimated to be twice as high as that in treatment plant effluents (Russell et al. 1982).

Most pollutants discharged into estuaries end up in particulate form through adsorption, complexation, and precipitation. Incorporation of pollutants in sediment deposits leads to concentrations that are much higher than in the overlying water (Neff et al. 1978). The possible deleterious effects of contaminant-bearing sediment on the benthos and organisms that feed on the benthos are a major concern (Risebrough et al. 1977).

California State agencies have been studying ways of determining local and

regional effects of waste discharges into San Francisco Bay (Johns and Bachman 1982). The substances of greatest concern have been petroleum hydrocarbons and heavy metals because samples of clams and mussels from the bay have shown some of the highest body burdens of these substances in organisms sampled from coastal waters nationwide (Luoma and Cloern 1982).

Past efforts to determine the effect of waste contamination on the biota of the bay have been limited largely to local studies of contaminant concentrations in individual organisms (Risebrough et al. 1977; Luoma and Cloern 1982; Luoma et al. 1985). With the increasing public awareness and concern about contamination and its effects, greatly expanded programs are being proposed. The State of California has established the non-profit Aquatic Habitat Institute to monitor and evaluate the effects of pollutant discharge on San Francisco Bay (California State Water Resources Control Board 1982). The National Oceanic and Atmospheric Administration (NOAA) of the U.S. Department of Commerce, as part of its long-term "National Status and Trends Program," is collecting sediments and bottom fish at three stations at each of four sites in San Francisco Bay annually to measure concentration of a variety of contaminants (National Oceanic and Atmospheric Administration 1986). This program will be expanded to include collections of bottom fish, sediments, and bivalves between three and six times per year for 2 years at a number of sites throughout the bay to measure trace contaminant concentrations and to conduct bioassay experiments (E.R. Long, National Oceanic and Atmospheric Administration, Seattle, WA; pers. comm.). Other agencies are planning additional pollutant-related studies (D.J. Baumgartner, U.S. Environmental Protection Agency, Newport, OR, pers. comm.; D.U. Palawski, U.S. Fish and Wildlife Service, Sacramento, CA, pers. comm.; S.E. Anderson, San Francisco Bay Regional Water Quality Control Board, Oakland, CA, pers. comm.).

5.3.1 Methods of Evaluation

Two approaches have been employed to study the effect of pollution on benthic organisms: the field survey and the laboratory bioassay.

Field population survey approach.

The results of numerous surveys of bay benthos during the past three decades, designed to show the extent of changes to the biota near waste outfalls and harbors, have been of only limited use in defining the effects of pollutant discharge on benthic communities. Early studies (e.g., Filice 1959) demonstrated the depressive effect of untreated industrial and domestic waste on the distribution and abundance of resident species. More recently, some local effects of sewage spills (Cloern and Oremland 1983), oil spills (Chan 1972, 1974), and poorly treated industrial discharges (Luoma and Cloern 1982), which cause local contamination of individual organisms and occasionally the local elimination of species populations, have been distinguished. Further, nearly all recent surveys in harbors and near outfalls also report the prevalence of animals typical of disturbed environments elsewhere, such as opportunistic species of the polychaete genus Capitella (e.g., Figure 33). There are, however, no data that suggest a progressive change in species composition and relative abundance among species during the past three decades even though the amounts of wastes are presumed to have steadily increased because of population and industrial growth (Nichols 1973). It is not clear whether this lack of perceived change means that there has actually been no effect from pollution, that pollution-related change has gone unnoticed, or that we are unable to distinguish pollution-related change from the sometimes opposing effects of natural factors.

There is much evidence from studies elsewhere that sediment contaminants may affect reproduction, growth, or survival of individuals. Yet such effects are almost never detected in quantitative population surveys in San Francisco Bay because the potentially important sources of variation in population size among samplings are numerous and difficult to separate. It is impossible to detect, for example, whether observed seasonal variations in the invertebrate populations on a South Bay mudflat (Nichols and Thompson 1985a) are due to seasonal variations in contaminant inputs from a nearby sewage treatment plant (see Thompson et al. 1984, Luoma et al. 1985), to natural physical disturbance of the sediment (e.g., wind-wave erosion), to predation, or to

interspecific interactions. Thus the significance of chronic, low-level contamination to San Francisco Bay benthic populations (as opposed to the individual organisms or their tissues, in which effects can be seen) remains uncertain (Nichols et al. 1986).

Comparing polluted versus control sites. One approach to assessing effects of waste effluents is to compare benthic community structure (species occurrences, abundance, biomass, diversity, similarity indices, animal-sediment interactions) at an effluent discharge site with that of a

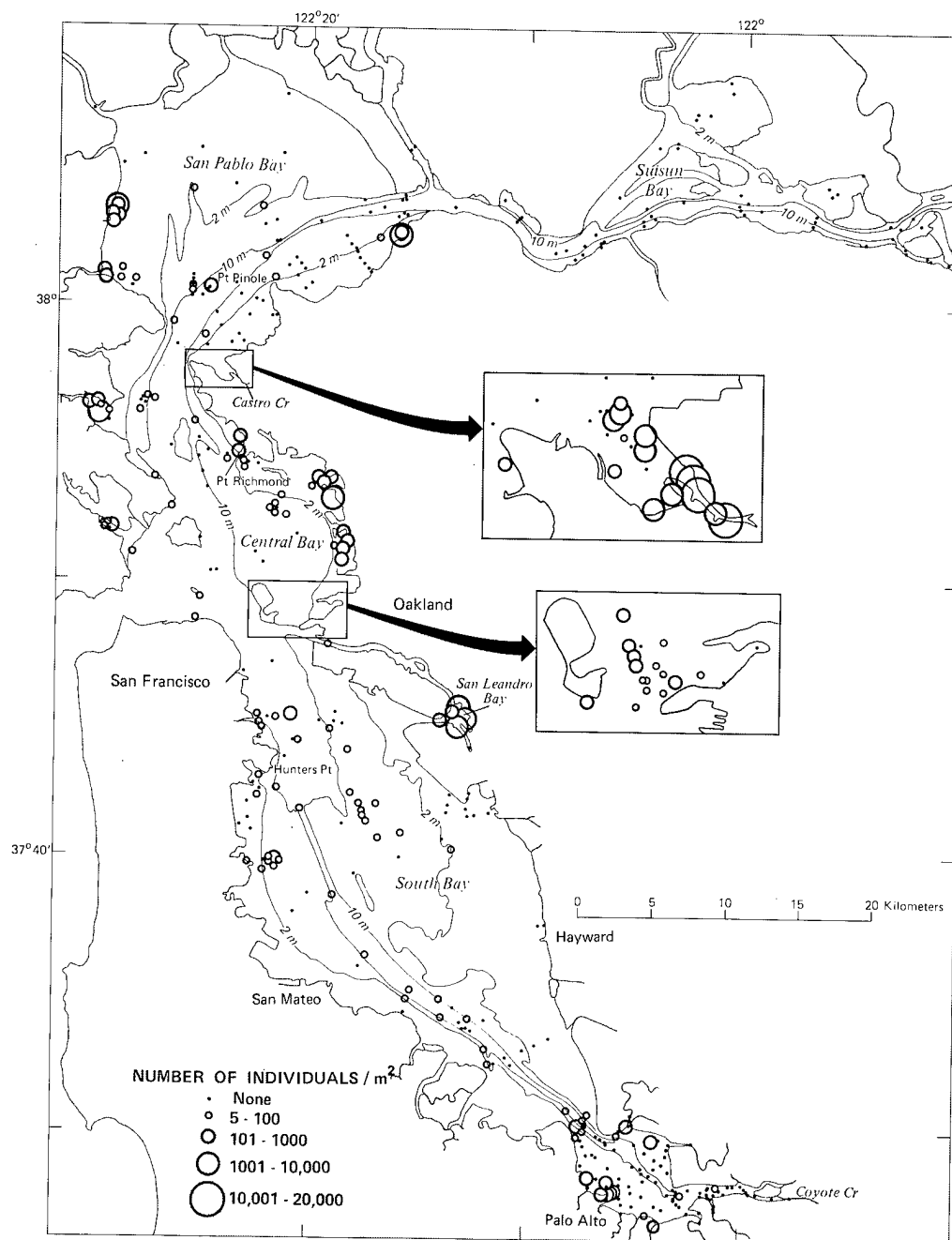


Figure 33. Distribution and abundance of *Capitella* species from results of many quantitative surveys summarized by Hopkins (1986).

site that is known to be nearly identical except for the absence of a pollutant source. In a typical example, samples collected each season from Castro Cove (a site contaminated with oil, chemical, and domestic waste) were compared with samples from Gallinas Cove and the Corte Madera Ecological Reserve (Figure 4), sites with similar physical characteristics, to determine differences in community and population indices (CH2M-Hill 1982). As might be expected, there were similarities and differences in community structure among the three sites. Some stations at the contaminated Castro Cove site were found to have fewer species; a greater abundance of *Capitella* spp., *Streblospio benedicti*, and *Polydora ligni*; fewer epibenthic crabs, shrimp, and fish; and greater mortality and higher body burdens of hydrocarbons in the marsh-dwelling mussels than those from the control sites. However, the results do not necessarily represent the effects of pollution alone. The large fluctuations in numerical abundance of individual species from one sampling date to another strongly suggest the importance of other sources of variation. Differences between sites could have resulted from differences in (1) sediment erosion, resuspension, and deposition that would, in turn, affect primary production and the food supply to the benthos, as well as reproduction, larval recruitment, and mortality; (2) freshwater intrusion and residence time over the mudflat and its possible effect on reproduction and mortality of benthic organisms; and (3) type, occurrence, and magnitude of predation.

Numerous similar studies worldwide, although conducted using the best available procedures and practices, have failed to show unequivocal effects of chronic nonlethal contamination of individuals (as in Johansson et al. 1986) or benthic populations because other factors are either overlooked, or cannot be controlled under natural field conditions. Sublethal effects on reproductive capacity, reproductive success, growth, and behavior can probably be conclusively demonstrated only through rigorously controlled experiments in which other factors that cause similar effects in the field are controlled or eliminated.

Tissue-contaminant survey approach.
On the grounds that the pollutant content of tissues indicates the incidence and

relative concentrations of the substances in their environment, mussels have been used worldwide as "sentinel organisms" for monitoring pollutants in coastal waters (Goldberg et al. 1978; Stephenson et al. 1979; National Academy of Sciences 1980; Goldberg 1986). However, the use of body burdens as indicators of pollution and stress to the organism is complicated by many factors (Luoma et al. 1985). Tissue burdens of silver in the clam *Macoma balthica*, for example, are highly dynamic (Figure 34), varying between seasons as much as fiftyfold from the combined effects of (1) seasonally fluctuating metal load in surface runoff, (2) varying spatial distribution of metals in the sediment, (3) an interaction between metal concentration and organism growth, and (4) an effect of freshwater inflow on metal bioavailability through its effect on sediment-water chemistry or residence time of water over the mudflat (Thomson-Becker and Luoma 1985). Elevated tolerances to trace metals have been observed in populations of *Macoma balthica* from metal-contaminated locations in San Francisco Bay (Luoma et al. 1983), implying the importance of adaptive flexibility to the survival of some populations. On the other hand, studies near a South Bay sewage outfall indicate that physiological stress caused by trace metal contamination occurs even in highly adaptable bivalves during periods when metal availability is highest (Johansson et al. 1986).

Body lesions, internal histopathological abnormalities, and high incidence of

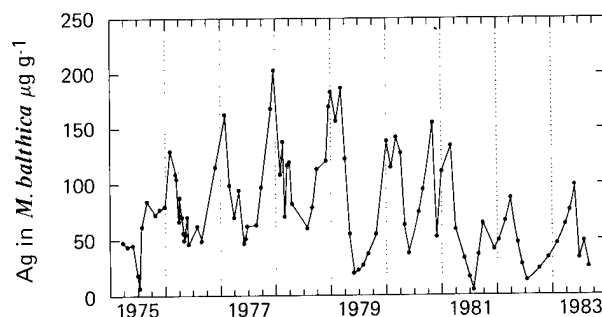


Figure 34. Concentrations of silver in *Macoma balthica* from the Palo Alto study site (from Luoma et al. 1985).

parasites and diseases in striped bass caught in San Francisco Bay may be indications of pollution effects on fish (Jung et al. 1984). Although similar histopathological abnormalities have been reported in benthic invertebrates in the New York Bight sludge disposal sites (Rosenfield 1976), similar afflictions of benthic invertebrates from San Francisco Bay have not been reported.

Laboratory bioassay versus field sampling approach. Bioassays are controlled experiments in which test organisms, under static or flow-through conditions, are subjected to different levels of particular pollutants (e.g., Marine Bioassay Laboratories 1984). Because of methodological constraints, the test conditions are often unnatural for the organisms (e.g., infaunal worms, clams, and crustaceans held in water without sediment or held in sediment that is unnaturally clean and devoid of other organisms), thus eliminating possibly important species interactions. Experiment durations are usually too short (a few days to a few weeks) to detect chronic effects on all life stages. Moreover, tests have been applied to only a few selected species known to be amenable to laboratory experimentation, but whose responses may be quite different from those of resident species. Finally, one substance alone may not produce the same results as combinations of substances, because of synergistic or antagonistic effects. Thus, it is not certain, even in carefully designed studies (e.g., McIntyre 1977) that observed sublethal or lethal effects under bioassay conditions will also occur in the field. For these reasons, most studies of pollutant effects in San Francisco Bay have used the field approach (Nichols 1973; CH2M Hill 1982).

Recently, bioassays (exposure of four test organisms in four separate procedures to natural sediment from three test sites in San Francisco Bay) were combined with sediment chemistry measurements and infaunal community analyses ("sediment quality triad"; Long and Chapman 1985; Chapman et al. 1986) to test the efficacy of such a program for use in the U.S. Department of Commerce national coastal/estuarine environmental monitoring program ("National Status and Trends Program"; National Oceanic and Atmospheric Administration 1986). Although the specific causes of faunal differences

among the sites sampled within the estuary were not clearly determined, the relative importance of anthropogenic factors at each site (sediment contamination, deleterious effects of sediments on test animals) could be inferred from the combined triad results: a waterway adjacent to the City of San Francisco was clearly the most pollution-degraded site, an open water site in San Pablo Bay was the least degraded, and an Oakland outer harbor site was degraded to an intermediate degree. Chapman et al. (1986) concluded that all three measures (sediment chemistry, sediment bioassay, community analysis) are "...necessary to determine the presence and measure the degree of contamination and of synoptically measured biological effects at each station and site."

Field bioassay. One variant of the bioassay approach is derived from the fact that organisms stressed by pollutants or high temperatures typically show reduced capacity for growth and reproduction (Bayne et al. 1982). The approach involves exposing test organisms in the field to known environmental pollutants. Subsequently, the total amount of ingested energy and the fraction retained by the organisms for somatic growth and gamete production (= scope for growth [SFG]; Warren and Davis 1967) is measured in the laboratory. This combined approach has been used in San Francisco Bay focusing on pollution gradients (using mussels, Martin et al. 1984), or thermal stress gradients at power plant effluent sites (using clams, Foe and Knight 1985b).

In principle, the rationale behind SFG has merit, but the methods used in San Francisco Bay studies (the laboratory measurements of respiration and ingestion and the statistical calculations of SFG) can be criticized for the lack of pollutant-body-burden data that could be correlated with pollutants actually present in the field and, thus, the lack of evidence that differences in SFG were indeed caused by pollutants or stress. (Unfortunately, even when body burdens of pollutants are known, one is still not sure whether observed increases in body burdens of pollutants and demonstrated lowering in SFG are related.) Another source of concern is that the transplantation of test organisms to and from polluted or nonpolluted sites itself had an effect on SFG (e.g., in the case of mussels, from Tomales Bay outside San

Francisco Bay to San Francisco Bay; Martin et al. 1984). Finally, if the results of SFG experiments were indeed valid for the test organisms, it does not necessarily follow that the results apply to other species in the benthic community. Some species thrive in polluted harbors, perhaps through genetic plasticity (Luoma 1977) and/or through constant recruitment from outside the affected area.

5.3.2 Sewage-Induced Nutrient Enrichment

An important consideration in the management of estuaries is the degree to which they are affected by eutrophication and the often-associated decrease in bottom-water oxygen content. In many estuaries, elevated nutrient inputs from sewage-treatment plants and runoff result in nuisance blooms of phytoplankton and macroalgae (e.g., Wilkinson 1963; Sawyer 1965; Soulsby et al. 1978). Widespread macroalgal blooms have occurred in San Francisco Bay (Section 4.2.2) and, in the one instance when benthic samples were being collected simultaneously, caused mass mortality of infauna by cutting off oxygen supply to the sediment (Section 3.2.1). However, a relation between enhanced macroalgal production and sewage-derived nutrient enrichment of the bay has not been demonstrated.

Waste nutrient-stimulated phytoplankton blooms that deplete dissolved oxygen, while important in many locations (e.g., Chesapeake Bay; Officer et al. 1984), also do not occur in San Francisco Bay despite high rates of waste-derived nutrient inputs (37×10^3 tons/yr nitrogen, 13×10^3 tons/yr phosphorus; Russell et al. 1982). Nutrient levels in South Bay are high each summer, particularly because wastewater from treatment plants is the major source of freshwater during summer and water residence time is high (Conomos et al. 1979). There have been no overt signs of eutrophication, however. One difference between San Francisco and Chesapeake Bays is the greater phytoplankton production in the latter (Peterson et al. 1985), leading to higher rates of bottom-water and sediment oxygen uptake (range of 8 to 106 mmol O_2 /m²/d in Chesapeake Bay [Kemp and Boynton 1981], versus 11 to 46 in San Francisco Bay [Hammond et al. 1985]). The greater depth and water column stability of Chesapeake Bay are also major factors

contributing to summer bottom-water anoxia.

Although accidental discharges of raw sewage occasionally cause local occurrences of oxygen depletion in San Francisco Bay (e.g., Cloern and Oremland 1983), the bay is generally well oxygenated throughout the year due to its shallow depth, and wind- and tide-induced mixing that keeps the water in close equilibrium with the atmosphere (Chapter 1; Hartman and Hammond 1985). Further, benthic grazing may significantly control the size of phytoplankton populations (Section 2.5.1), thus preventing the accumulation of critically large biochemical oxygen demand (Nichols et al. 1986). Cloern et al. (1985) have shown that the most intense blooms are concentrated in the shallow areas of both the northern and southern ends of San Francisco Bay, where active grazing within the photic zone by the shallow-water benthos would be expected to be most intense. The limiting effect of wind-generated turbidity and vertical mixing upon the amount of available light for photosynthesis may also be a factor in preventing large phytoplankton blooms (Cole and Cloern 1984).

5.3.3 Effect of Pollution on Benthic Community Metabolism

The size of microbial and faunal populations in sediments and the activity of the total community as measured in terms of sediment oxygen uptake generally increase as the supply of organic matter to the bottom increases. Polluted waters with high organic loading show relatively high rates of oxygen consumption (Stein and Denison 1966; Pamatmat et al. 1973; Smith et al. 1974). On the other hand, the presence in sediments of noxious chemicals that affect respiration should be reflected by low benthic community metabolism. Nonetheless, even grossly polluted areas such as the New York Bight sludge disposal site show high rates of oxygen uptake (Thomas et al. 1976), undoubtedly due to the amount of organic material being deposited there.

We do not know if the pollutants in San Francisco Bay sediments inhibit benthic community metabolism. A possible way of detecting such an effect indirectly might be to compare the San Francisco Bay data of Hammond et al. (1985) and Cole and

Cloern (1984) with Hargrave's (1973) empirical equation relating benthic oxygen consumption to plankton primary production and mixed layer depth (Section 4.7). The oxygen uptake at the deeper station of Hammond et al. (1985), where annual net primary production is 150 g carbon/m² (Cole and Cloern 1984) and the entire 14-m deep water column is well mixed, is predicted by the equation to be 120 liters O₂/m²/yr. By comparison, the annual average rate of benthic oxygen consumption calculated from actual measurements was 130 liters O₂/m². It would seem, therefore, that San Francisco Bay does not differ from the other ecosystems in regard to the relation between benthic metabolism and plankton primary production. Such a comparison is tenuous, however, because we cannot rule out the possibilities that (1) Hargrave's (1973) equation may have included results from ecosystems affected by pollution, and (2) that any inhibitory effect by pollutants on San Francisco Bay benthic community metabolism is masked by an enhancing effect resulting from the unmeasured supply of organic matter represented by detritus derived from such sources as sewage, wetlands, and benthic microalgal production.

5.4 SEDIMENT BUDGET AND DREDGING

Each year, large quantities of mud and sand are carried into San Francisco Bay from the drainage basin. This material has historically represented a nuisance in the maintenance of navigable channels and harbors. On the other hand, there are concerns about the effects of the removal and deposition of the dredged material on the bay's living resources.

5.4.1 Estimates of the Sediment Budget

Although annual suspended sediment input to San Francisco Bay varies with the rate of inflow from the two major rivers, a long-term average is estimated at 8×10^6 m³ (Krone 1979). Estimates of the fraction of this total that is discharged to the ocean vary widely (4%, Gilbert 1917; 6%, Conomos and Peterson 1977; 50%, Krone 1979), demonstrating how little we understand the bay's sediment budget. Typically, much of the winter sediment load in the Sacramento-San Joaquin Rivers settles out in San Pablo Bay. In summer,

wind waves and tidal currents erode the previously deposited sediment and redistribute it over a wider area of northern San Francisco Bay. In South Bay the shallow reaches seem to be experiencing net erosion, while the deeper channels are filling (Fuller 1982).

A total of about 7.6×10^6 m³ of sediment is dredged annually to maintain navigation channels in San Francisco Bay (Sustar 1982). Thus, the average total amount of sediment dredged from the bay each year is about equal to the average annual sediment input estimated by Krone (1979). Such an equality suggests that, to the degree that new sediment entering the bay is deposited outside these channels (i.e., on the shallow shoals), dredged material is sediment that is simply moving (by means of tidal, gravitational, and wind-driven water circulation) from one place in the bay to another. Because disposal of most of the dredged sediment occurs at three open water sites within the bay (one site at the western end of Carquinez Strait, one near the southwestern end of San Pablo Bay, and one near Alcatraz Island in Central Bay; Fong et al. 1982), it is also probable that some of this recirculating sediment includes sediment that has been dredged before.

5.4.2 Effects of Dredging on the Benthos

The environmental effects of dredging and disposal of dredged sediments have been widely reviewed (O'Neal and Sceva 1971; Morton 1977; U.S. Army Corps of Engineers 1977; DiSalvo 1978; Hirsch et al. 1978). The Corps of Engineers has developed procedures for assessing the possible impacts of proposed new dredging in San Francisco Bay (Fong et al. 1982).

A typical scenario for dredging and its impacts is as follows. During the course of dredging as well as the subsequent dumping, the water becomes turbid with resuspended silt and clay, and dissolved oxygen is consumed (JBF Scientific Corporation 1975; U.S. Army Corps of Engineers 1976), although the effects are usually greater during disposal than during dredging (U.S. Army Corps of Engineers 1976). The formation of a thick suspension of dredged sediments called fluid mud smothers some species but not

others (Diaz and Boesch 1977). The resulting turbidity is relatively short-lived and probably no worse than the natural turbidity caused by winter river discharge, wind waves, and tidal currents. Laboratory studies of the effect of sediment suspensions on mussels, clams, worms, and crustaceans (Peddicord et al. 1975) show that the mud-dwelling invertebrates would not be harmed by field suspensions noted during actual dredging operations in the bay (U.S. Army Corps of Engineers 1976). The depression of dissolved oxygen concentration is small and brief, probably because the bulk of the sediment rapidly sinks to the bottom before all the reduced substances can be oxidized. Advection and mixing quickly restore equilibrium conditions.

The dredged bottom, as well as the dumped deposit, are usually recolonized rapidly (McCauley et al. 1977). Moreover, the areas of dredging and deposition at any one time are small fractions of the total area of the estuary. Thus, the influx of organisms from the surrounding undisturbed areas can be rapid. Additionally, benthic communities normally subject to wave scour, high turbidity, and sediment redeposition rapidly recover from dredging and sediment disposal because the residents are rapidly reproducing opportunistic species with short life cycles (Oliver et al. 1977). Because many of the species in San Francisco Bay remain reproductively active for much of the year (Section 3.1.1), they can quickly colonize a newly exposed sediment surface. As a result, San Francisco Bay benthos can be expected to be as resilient as that in other estuaries (Boesch et al. 1976).

5.4.3 Effects of Contaminated Dredged Sediments on Organisms

Resuspension of sediment, enriched relative to the overlying water, with a large variety of substances including waste chemicals, could cause harm not only to benthos, but to plankton as well. However, resuspension of sediment deposits can remove as well as liberate substances, depending upon pH, oxidation-reduction level, relative concentrations in sediment and water, and ion-exchange capacity -- factors that influence chemical processes such as acid-base balance, precipitation-dissolution, complex formation, oxidation-reduction, and adsorption reactions (Lee

1970). Sorption and release of substances depend on complex dynamics involving (1) diffusion of ions within sediment, (2) reactions in interstitial water, (3) humic binding forces, (4) organic/inorganic complexes, (5) nutrient mobilization, (6) reactions at the sediment-water interface, (7) mobility of cations from the sediment, and (8) water-sediment exchange reactions (Lu and Chen 1977).

San Francisco Bay sediments subject to dredging are contaminated with oil and grease discharged by refineries and other industrial plants (Citizens for a Better Environment 1983) and from urban runoff (Stenstrom et al. 1984). These contaminants include numerous natural and petroleum-derived hydrocarbons; fats, oil, and waxes of both natural and anthropogenic origin; fat-soluble materials such as the polynuclear aromatic compounds DDT and PCB; and elemental sulfur. Such substances differ in biodegradability as well as short- and long-term toxicity. Determining the effects of contaminated dredge spoils is usually difficult.

Shuba et al. (1978) concluded from an extensive study of highly contaminated sediments from Puget Sound, Long Island Sound, New York Harbor, James River, and Mississippi River, that toxicity of contaminated sediments to test organisms in the laboratory does not positively indicate the same toxicity in the field. Hughes et al. (1978), in a comparative study of benthic and epibenthic species population density and community composition at a dredge disposal site and a control site in Elliott Bay, Puget Sound, Washington, found that differences between sites could not be attributed to dredge spoils alone because many other factors (e.g., species migrations) were not considered in the sampling design.

In laboratory studies, mussels, clams, crabs, and snails from San Francisco Bay showed only minor uptake from sediment contaminated with oil and grease (DiSalvo et al. 1977). Anderlini et al. (1975), in an effort to measure the biological uptake of sediment contaminants (primarily heavy metals) suspected of being mobilized during dredging and disposal, compared body burdens of transplanted mussels and sediment macrofauna in dredge and disposal sites and in control sites. The organisms showed only

small changes in average metal concentrations.

In summary, studies to date of the biological effects of dredging and dredge spoil disposal and the toxicity of contaminants in the dredged material in San Francisco Bay, as elsewhere, have shown the following: (1) measured damage is apparently limited in duration and area affected; (2) while toxicants in sediments are accumulated by infauna and other organisms, and these substances cause stress and behavioral changes during bioassay experiments, there is no clear evidence to date that populations and communities have been adversely affected (e.g., that recovery is not complete); and (3) because different species show different effects from the same concentrations of toxicants, the only realistic experiments that apply to a specific estuary are those involving resident species and their responses to pollutants occurring there.

5.4.4 Effects of Channel Dredging on Salt Intrusion

San Francisco Bay, like other shallow estuaries where shipping is an important activity, requires maintenance dredging of midbay channels and harbors to counteract the constant deposition of sediment. Increasing ship size often necessitates further deepening of channels.

Channel deepening has important implications for circulation and mixing of bay waters in the northern reach between San Pablo Bay and the Delta. In particular, channel deepening in northern San Francisco Bay enhances upstream saltwater intrusion, thereby exacerbating the effects of reduced river inflow. Case histories of channel dredging to allow passage of deep-draft vessels (e.g., Rotterdam Harbor, van der Burgh 1968) and modeling studies (e.g., Festa and Hansen 1976) have demonstrated that increases in channel depth by a few meters can enhance gravitational circulation and increase by many kilometers the upstream extent of saltwater intrusion (Figure 35). Increased saltwater intrusion has obvious consequences for agriculture in the western area of the Delta by threatening freshwater supplies and contaminating the soil with salts. Such changes eventually result in long-term land-use changes (Hackney and Yalverton, in press).

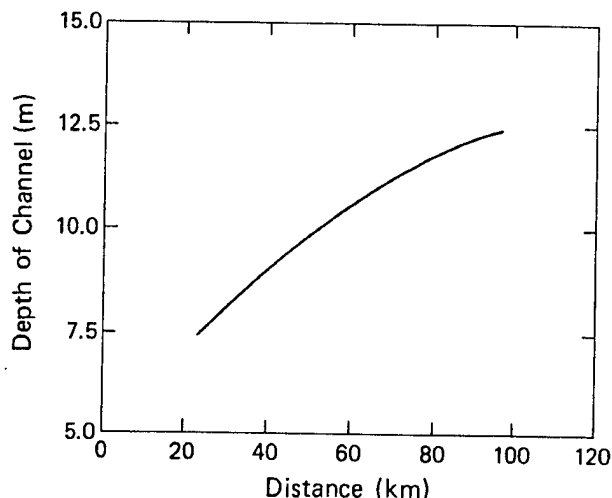


Figure 35. Relation between the depth of the river-estuary channel and the extent of landward intrusion of saltwater (0.05‰) under constant flow, from model results (adapted from Festa and Hansen 1976).

Increased saltwater intrusion also leads to altered species distributions that can have important secondary effects on the bay ecosystem. Hill and Kofoed (1927) recognized that it was the combination of channel deepening and low river flows during the periods of 1913-14 and 1919-20 that led to the spread of saline bottom water in northern San Francisco Bay; this, in turn, permitted the upstream migration of the introduced marine wood-boring shipworm *Teredo navalis*. The invasion of this pest species caused rapid and widespread destruction of the wood pilings in bridges and piers in the northern bay and Delta. Increased saltwater intrusion also encouraged the upstream migration of estuarine benthic filter feeders into Suisun Bay during the 1976-77 drought, which resulted in a temporary shift from a primarily pelagic food web supporting important fisheries such as the striped bass, to a benthic food web of lesser economic significance (Sections 3.2.1, 5.2).

Although it is not possible to separate the effects of river flow reductions and channel deepening on saltwater intrusion, the results from studies elsewhere suggest that the latter effect cannot be ignored in discussions of the estuary's salt balance.

CHAPTER 6. SHELLFISHERIES

The shell middens that dotted the shoreline of San Francisco Bay until the beginning of the present century (Figure 31) provided visible evidence of the importance of shellfish to the aboriginal inhabitants of the bay area before the arrival of Spanish soldiers and missionaries (Nelson 1909). Composed largely of the bay mussel, Mytilus edulis, and the bent-nosed clam, Macoma nasuta, in the northern part of the bay, and the native oyster Ostrea lurida in the southern part, the shell middens were the residences, refuse heaps, and burial grounds of a culture dependent to a large degree on local shellfish. Large-scale harvesting of shellfish by the post-Gold Rush settlers continued into the early years of the present century until the shellfish beds became fouled by human and industrial wastes. Today there is hope that shellfisheries will once again become prominent in San Francisco Bay.

6.1 EARLY HISTORY OF BAY SHELLFISHERIES

6.1.1 Oysters

J. E. Skinner, in his review of the history of San Francisco Bay's fish and wildlife resources (1962), pointed out that the bay "undoubtedly possesses the greatest potential of any area in the State [California] for shellfish culture." To the immigrants of the 1850's, the broad expanses of intertidal and shallow subtidal mudflats seemed ideal for shellfish growing. Unfortunately, the native species were, for the most part, not favored: "Native oysters [Ostrea lurida], with their small size, rather dark meat, and strong, coppery flavor, did not appeal to easterners accustomed to the larger, whiter, and milder oysters" (Barrett 1963). Thus, although the native oyster was commercially harvested in San

Francisco Bay, no attempt was made to cultivate it there (Bonnot 1935, Barrett 1963). The same species was imported by ship from Shoalwater Bay, Washington (now Willapa Bay), beginning in 1850, because it was successfully cultured there. This enterprise, known as the "Shoalwater Trade," provided most of the oysters for San Francisco until the late 1860's, although oysters from other Pacific coast locations, e.g., Mazatlan oysters from Mexico, were also imported during this period.

With the completion of the transcontinental railroad in 1869 came the opportunity for growing oysters in San Francisco Bay on a large scale. The introduction of the eastern oysters, Crassostrea virginica (Section 2.3), created an industry that, by the 1890's, became the most important fishery in California. At its peak in 1899 the industry produced nearly 3×10^6 lb of meat per year (Skinner 1962; Barrett 1963). Because the eastern oyster never reproduced in commercial numbers in the bay, the industry depended on the continuous import of eastern seed oysters. Despite this obstacle, San Francisco Bay remained the Pacific coast center of eastern oyster growing for many years.

Most of the oyster beds were located in the shallows of South Bay (Figure 36); the low salinity and the high rates of siltation in winter (particularly during the period of hydraulic mining; Gilbert 1917) apparently precluded good oyster growth and survival in the northern part of the bay. The beds were fenced with closely spaced stakes to keep out predators (Barrett 1963).

The first signs of problems in the bay's oyster industry appeared about 1900, as the oysters grew more slowly, became thin and watery, and often were unfit for

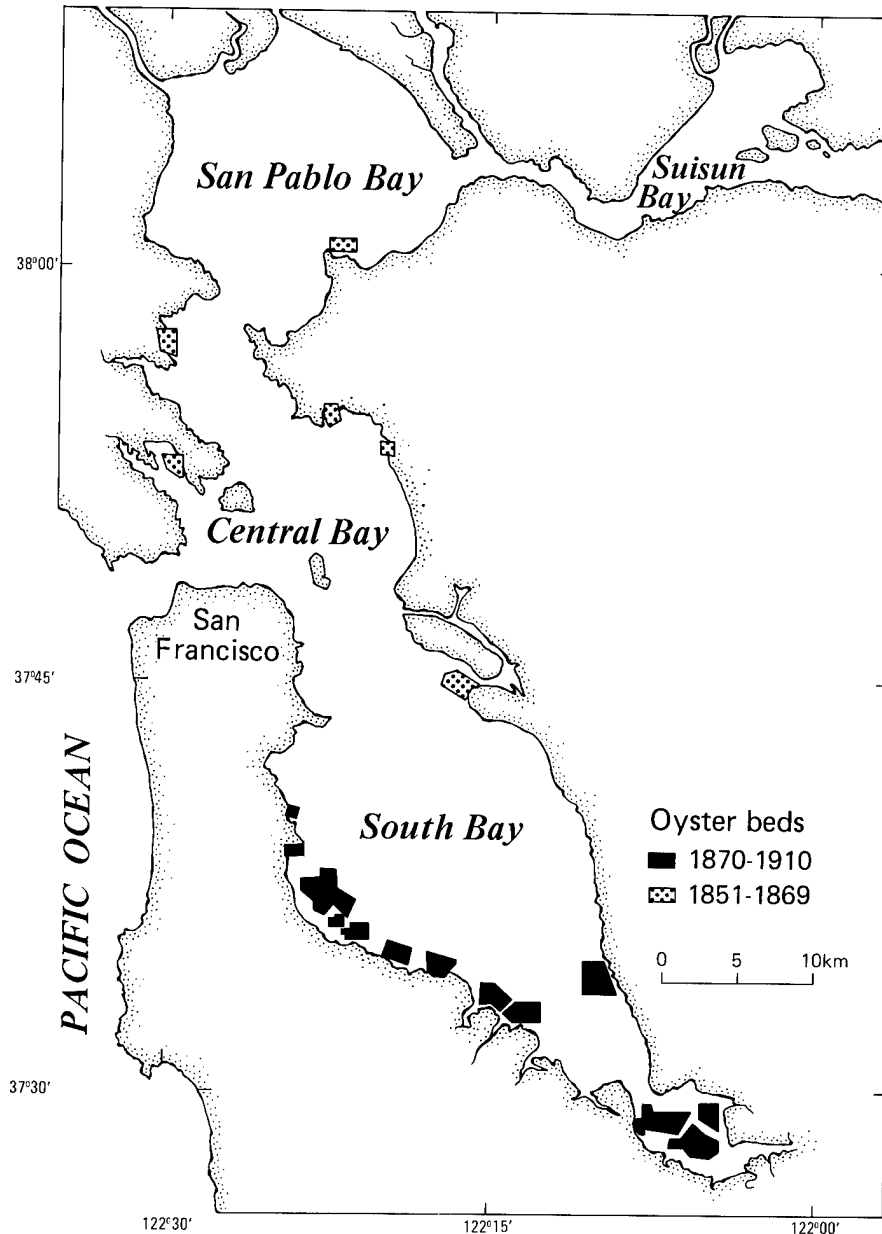


Figure 36. Location of former oyster beds (Barrett 1963).

sale (Bonnot 1935). Observers at the time (Nelson 1909) attributed the deterioration of the oysters to the untreated human and industrial wastes being discharged into the bay. By 1910, seed oysters were no longer being imported from the East coast, and by 1935 the oyster industry in San Francisco Bay had collapsed (Bonnot 1935; Skinner 1962). Bonnot concluded that "Portions of San Francisco Bay are free from sewage but great areas are contaminated and must be avoided. In clean

areas where native oysters develop to commercial size, some effort may be made to improve natural conditions but no great amount of time or energy should be spent in San Francisco Bay until sanitary conditions improve" (Bonnot 1935).

While the live native oyster fell into disfavor, its shells did not. The ancient deposits of shell material and associated mud provided a ready source of the materials used to make cement

(calcium, magnesium, silica, aluminum, iron, etc.) as well as livestock and poultry feed (Hart 1966). Between 1924 and 1966, large-scale dredging of the shell deposits, largely located in South Bay (Figure 9), removed an estimated 30×10^6 tons of shells (Hart 1966). The practice continues to the present on a smaller scale.

6.1.2 Clams and Mussels

The shell deposits in the Indian middens around the bay suggest that the bay mussel, Mytilus edulis, was abundant enough in the earlier centuries (Nelson 1910) that as much as one-third of the harvest was carried upstream to the villages of the Sacramento-San Joaquin River Delta (Cook 1946). In the upper, more recent layers of the shell middens, the bent-nose clam, Macoma nasuta, becomes prominent. Whether the gradual shift from Mytilus to Macoma resulted from a change in their relative abundance or a change in aboriginal food preference is not known.

The Gold Rush immigrants did not consider these native species worthy of large-scale commercial exploitation within the bay. Nonetheless, the bent-nosed clam, dug in large numbers in South Bay by Chinese shrimp fishermen, was common in the San Francisco markets in the decades following the Gold Rush (Fisher 1916). The bay mussel, Mytilus edulis, also contributed significantly to the total mollusk landings from the bay in the late 1800's (Skinner 1962). The accidental introduction of the eastern soft-shell clam, Mya arenaria, sometime between 1869 and 1874 (Carlton 1979a), led to its gradual replacement of native species in the marketplace (Fisher 1916) and contributed to a greatly expanded mollusk fishery. Fencing of the clambeds to prevent predation by rays and flounders greatly enhanced the soft-shell clam harvest (Bonnot 1932a). At the peak of this fishery in the 1880's and 1890's, between 1 and 3 million lb of Mya meat were harvested annually (Skinner 1962). The harvest gradually declined thereafter: between 1916 and 1935 it ranged from 100,000 to 300,000 lb per year, then fell off rapidly. By 1949 the catch was negligible, and records were not kept thereafter (Skinner 1962).

The decline in the clam fishery was attributed to increasing labor costs to

harvest the clams and the pollution or filling of clam beds (Bonnot 1932a; Skinner 1962; Wooster 1968a). Bonnot (1932a) noted that some of the clam beds were "abandoned due to industrial wastes which are dumped into the bay." During that same year (1932) the California State Board of Public Health established a permanent quarantine on clams in San Francisco Bay "by reason of sewage pollution . . . and consequential danger of typhoid fever and gastro-enteritis" (excerpt from Minutes of May 28, 1932). The general quarantine was later rescinded (1934) and replaced with a quarantine that covered only a few specific polluted locations within the bay. In 1945 the original quarantine was put into the California Department of Public Health administrative code (apparently in ignorance of the 1934 rescission); in 1953, at the request of a clamming company that wished to dredge for clams in the middle of the bay, the codified quarantine was itself rescinded (Jones and Stokes Associates, Inc. 1977). Today, no general quarantine of shellfish is in effect.

The Japanese littleneck clam, Tapes philippinarum, accidentally introduced to the west coast of North America with Japanese oysters sometime in the 1930's and 1940's, was discovered in San Francisco Bay in 1946 (Carlton 1979a). This species thrived and became the focus of sport harvesting that continues to the present.

6.1.3 Crabs

At the time of the Gold Rush, the market or Dungeness crab, Cancer magister, was incidentally collected from San Francisco Bay in fish nets. In the 1860's, crabs caught in the bay were marketed in San Francisco (Dahlstrom and Wild 1983). The bay's crab fishery declined thereafter because the crabs were small and abundance was too low to support the fishery; by 1880 the fishery was forced offshore (Dahlstrom and Wild 1983). The offshore fishery remained an important industry until 1960 when a precipitous and permanent decline occurred. The decline is variously attributed to a change in ocean climate (i.e., increased water temperature and intensified currents), predation by hatchery-reared silver salmon Oncorhynchus kisutch, and pollution (Wild and Tasto 1983). Some juveniles still use the bay as a nursery and feeding ground.

6.1.4 Shrimp

Bay shrimp, Crangon franciscorum, C. nigricauda, and C. nigromaculata, were first exploited by Italian seine fishermen in 1869. These fishermen were soon put out of business by Chinese shrimp fishermen employing ancient Chinese techniques that included use of fine-meshed nets (Bonnot 1932b; Skinner 1962). The larger specimens were sold in local markets, but the bulk of the catch was dried and shipped to China (Bonnot 1932b). The loss of many juveniles of commercial fish species in the Chinese shrimp nets resulted in the imposition of closed seasons, restrictions of the industry to limited areas of the bay, and limitations on the amount exported (Bonnot 1932b). Despite the limitations, the catch in 1929 exceeded 3×10^6 lb, then declined owing to a lack of suitable markets. The fishery was revived on a small scale in 1965 to supply bait for sportfishermen (Smith and Kato 1979).

6.2 PRESENT STATUS OF BAY SHELLFISHERIES

6.2.1 Sport Harvesting of Mollusks

Despite the possibility of contamination from wastes (particularly during winter when urban runoff increases and sewage treatment plants occasionally overflow) and the lack of official authorization, sport harvesting of shellfish from the bay's intertidal beds continues (McAllister and Moore 1982). The primary focus of sport clamming in the bay is the Japanese littleneck clam, Tapes philippinarum, although Mya arenaria, Mytilus edulis, and a variety of much less common species are taken as well. While Tapes is collected primarily as food, a large percentage is used as bait by fishermen.

In 1967, Wooster (1968a,b) conducted the only known baywide survey of intertidal shellfish beds. He identified the major beds, including five native oyster beds, and determined the abundance of individual species in each. He estimated a total abundance of 21×10^6 adult Mya, Tapes, and other assorted species in beds baywide, an abundance sufficient to support 2×10^6 person-days of recreational shellfishing per year.

Recent surveys of the most promising of the bay's shellfish beds (Sutton 1978; Sutton and Jefferson Assoc. Inc. 1981; McAllister and Moore 1982) demonstrate the great potential for shellfish harvesting in the bay as well as the present importance of this source of food to some bay area residents. Large numbers of Tapes and occasionally Mya are found in discrete intertidal beds, particularly along the eastern and western margins of central South Bay in the narrow band of rock, cobble, and broken concrete riprap along the base of dikes, piers, and breakwaters (Figure 37). In other words, an "introduced" habitat, in areas that formerly were marshes or open mudflats, provides the appropriate substrate for the introduced mollusk species that constitute the bay's only clam fishery. Much less is known about subtidal shellfish populations, although various sampling efforts have shown that South Bay contains Tapes populations that might be commercially exploited (McAllister and Moore 1982).

6.2.2 Commercial Harvesting of Crustaceans

Although there is no longer a Cancer magister crab fishery in the bay, two



Figure 37. Breakwater of boulders, broken concrete, and cobble that provides habitat and refuge for Tapes philippinarum and Mya arenaria.

other commercial crustacean fisheries operate in the bay: the bait shrimp and brine shrimp fisheries. The bay shrimp, Crangon franciscorum, C. nigricauda, and C. nigromaculata, are commercially fished with beam trawls, primarily in Suisun and San Pablo Bays and the extreme south end of South Bay, to provide bait for striped bass and sturgeon sport fishing (Frey 1971; Smith and Kato 1979). The small size of these shrimp apparently limits their usefulness as food for human consumption.

The brine shrimp, Artemia salina, is abundant in the shallow diked ponds bordering South Bay where salt is produced by solar evaporation. This species thrives under the hypersaline conditions of the salt ponds, and 250 to 375 tons are harvested per year to provide food for aquarium fish (Bay Conservation and Development Commission 1986). In addition, brine shrimp eggs from the salt ponds are shipped worldwide to be hatched and used as fish food and for use in laboratory research.

6.3 THE FUTURE OF BAY MOLLUSK FISHERIES

6.3.1 Oysters

Although oysters have not been grown commercially in the bay for many years, recent field tests by the California Department of Fish and Game (McAllister and Moore 1982) and by the Morgan Oyster Company (unpubl.) have shown that oysters suspended above the bottom on racks would grow well enough to permit the reestablishment of an oyster industry (Bay Conservation and Development Commission 1986). The major obstacles to commercial oyster growing in the bay seem to be (1) developing a sufficiently large market for bay oysters to return the investment required to cover land acquisition and operational costs, and (2) meeting health standards with regard to tissue contamination. Oysters grown commercially in the bay would require depuration--holding the oysters in a controlled clean-water en-

vironment until contaminants are reduced to acceptable levels. Such holding facilities are common worldwide wherever oysters are grown adjacent to urban areas (Jones and Stokes Assoc., Inc. 1977).

6.3.2 Clams

Commercial harvesting of clams from bay mudflats is apparently inhibited by high labor costs associated with digging. Moreover, the limited size of existing beds would preclude large-scale harvesting. Sport harvesting is expected to continue despite the lack of official authorization (McAllister and Moore 1982).

Recommendations for enhancing the sport shellfishery for Tapes philippinarum include planting of hatchery-produced seed clams and enlarging the clam habitat by covering potentially suitable intertidal mudflats with an appropriate mix of cobble, gravel, and shell materials (McAllister and Moore 1982).

6.3.3 The Threat of Pollution

Contamination of bay water, bottom sediments, and organisms by wastes remains the major concern preventing official approval of shellfish harvesting. Great strides have been made during the past 20 years in resolving many water quality problems. The operation of modern sewage treatment facilities around the bay has led to the near elimination of incidences of low dissolved oxygen, and the reduction of coliform (human waste) bacteria to very low levels in most locations during most of the year. Occasional treatment plant malfunctions do, however, sometimes cause contamination of some shellfish beds. Contamination with viruses and with trace organic and inorganic materials in industrial wastes persists and represents a potential threat to people who regularly eat bay shellfish (Jones and Stokes Assoc., Inc. 1977). Therefore, the California Department of Health Services does not officially permit shellfishing except under occasionally authorized, strictly controlled conditions as requested by local governments.

CHAPTER 7. MANAGING BENTHIC RESOURCES

7.1 INTRODUCTION

We have described in this profile the soft-bottom benthic environment in San Francisco Bay and have defined, where possible, the important features and processes that link the benthos with the rest of the estuarine ecosystem and with humans. It is clear that the benthos is an important component of the estuary and is a resource that has measurable economic value. The soft-bottom habitats of estuaries are places where both living and nonliving organic matter accumulates (Chapter 4) and subsequently becomes food for diverse bottom-living primary consumers from bacteria to clams (Chapter 2). The inconspicuous clams, worms, and small crustaceans living in the mud at the bottom of the bay are a major source of food for abundant and diverse predators (fish, sharks, rays, shrimps, crabs, and shorebirds) during at least some part of the predators' lives (Chapter 3). Humans have also exploited the productive bottom of the bay by harvesting both the primary consumers (clams, oysters) and secondary consumers (fish). The potential for renewed mollusk fisheries in the future (Chapter 6) has stimulated renewed interest in the bay's protection and management (e.g., McAllister and Moore 1982; Bay Conservation and Development Commission 1986). We have also used macroinvertebrates, because of their generally sessile lifestyle, as measures of the degree to which the estuary shows evidence of human alteration (Chapter 5). In short, the value of the benthos to an estuarine ecosystem is much greater than its direct monetary value.

Concerns about the present condition of the estuary and about the potential for further change and possible deterioration in its aesthetic and economic values need to be translated into good management policies and practices. However, because

of the divergent uses of and conflicting demands on the bay, decisions are difficult. Use of the bay as a site for waste disposal conflicts with the use of the bay as a source of food (fish, clams). Use of former wetlands for garbage dumps and commercial developments conflicts with aesthetic and recreational values and eliminates wildlife habitat. In order to develop appropriate policies and practices that can resolve such conflicts, it will be necessary, first, to educate managers and users (the public) about the recreational, economic, and aesthetic values of the estuary. Second, it will be necessary to overcome the obstacles (limitations of scientific understanding, threats posed by human activities, the lack of clear management policies and objectives, and the limited financial support for scientists, educators, and resource managers) that prevent us from protecting and enhancing bay resources and maximizing the human benefits obtained from them.

7.2 PUBLIC PERCEPTIONS, USES, AND CONCERNS

Cities bordering the bay have historically located their refuse dumps near the perimeter of the bay. Additional debris collects at the edge of the bay by tide and wind action. As a result, a visitor approaching the bay finds a disturbed, often unattractive sight at most points of access. Broken bottles (a few dating to the previous century and thus providing modern archeological treasures for bottle collectors), cans, refuse from fishing and pleasure boats, and automobile tires (Figure 38) litter the shore. In particular, that portion of the mud bottom of the bay visible at low tide (about 15% of the surface area of the bay, much of which is muddy and difficult to walk on, and thus frequented by only a small number of clamdiggers) has been viewed as an eyesore and a smelly nuisance to be filled

7.3 SCIENTIFIC BASIS FOR MANAGEMENT

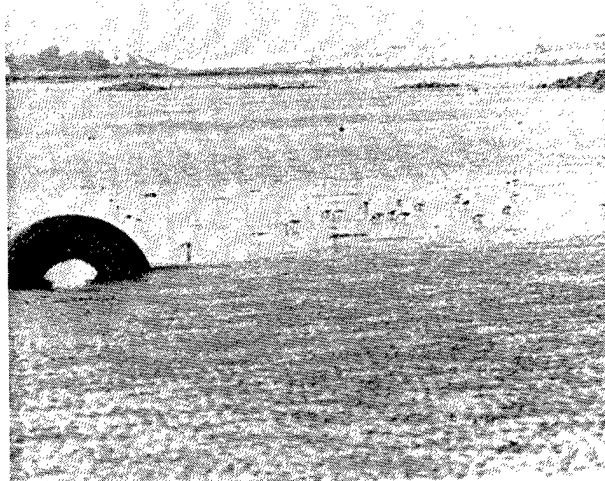


Figure 38. A typical bay view (photograph courtesy of D.R. Hopkins).

and put to a more "useful" purpose. Fortunately, within the past two decades that attitude has been changing (e.g., Bay Conservation and Development Commission 1983).

Although most of the land above high water is still fenced private or public land, ongoing efforts to develop bayfront trails and parks are greatly expanding public access. Additionally, a growing number of public educational facilities located around the shore of the bay feature displays and training programs about the natural history of the bay and surrounding area (for location maps of these facilities, see Bay Conservation and Development Commission and Institute for Human Environment 1981). These facilities are increasing public awareness of the bay, its various habitats, and biotic communities.

There is public concern that fish and shellfish, although still abundant in the bay, may not be safe to eat. Furthermore, there is concern that continued disposal of wastes as well as increased diversion of freshwater away from the estuary may lead to unwanted changes or declines in the bay's biota. Dealing with these concerns effectively requires that policy makers and the public have an appropriate level of scientific understanding.

7.3.1 Present Knowledge

In the preceding six chapters we have summarized the results of several decades of benthic research and monitoring. In summary, we have a good general understanding of many qualitative aspects of benthic ecology. We know how individual benthic species are distributed around the bay, we have some idea of their general ecology, and we presume that we know what they eat and who eats them (Chapters 2 and 3). We know that the benthos mineralizes organic waste, consumes microalgae perhaps to the extent that it controls nuisance growth, returns essential nutritive materials to the water column, and provides a major source of food for fish and aquatic birds. We also know that the benthos is sensitive to human activities such as waste disposal practices (Chapter 5). With this background, we can draw tentative, qualitative conclusions about probable relations (or lack of relations) between human activities and changes in the benthic environment.

It is apparent in nearly every chapter of this profile, however, that there are major gaps in our understanding. Our knowledge of the benthos is limited largely to macrofauna (we know almost nothing about the micro- and meiofauna of San Francisco Bay). Moreover, detailed understanding of the macrofauna itself is lacking in many areas. We have very little quantitative understanding of many of the physical, chemical, and biological processes that determine the nature of the benthic community at any site. In particular, we have only qualitative understanding of the importance of physical processes (e.g., freshwater inflow, water circulation and mixing, patterns of temperature and salinity variations) to observed variations in the distribution and abundance of benthic macrofaunal animals. Achieving quantitative understanding is critical if we are to correctly anticipate the effects on the benthic environment of, for example, proposed development project alternatives.

We know little about the pathways and rates of organic matter inputs to the benthos and about what or how fast the animals eat. We also have little specific

knowledge of the rate of predation by other invertebrates, fish, or birds on benthic species, and of the importance of predation relative to other sources of invertebrate mortality. We do not know how critical the abundance of benthic invertebrates is to consumer populations such as fish. We do not know to what degree contaminants affect benthic populations or the consumers of those populations. Finally, we do not know if the benthos of the bay is changing with time as a result of increasing human influence.

Nonetheless, these kinds of information are critical to rational management of important benthic resources and of the estuarine system as a whole. Knowledge gained from other estuaries helps us to gain insight into San Francisco Bay processes and problems, but again, only in a qualitative sense. Management of an individual estuary such as San Francisco Bay requires quantitative understanding developed in that estuary.

7.3.2 Hindrances to Increased Understanding

The limitations of our knowledge of benthic processes, like most other estuarine processes of the bay, stem largely from an historic reluctance to invest significant financial and human resources toward their study. This reluctance derives, in turn, from (1) the lack of public appreciation that the estuary, like any natural resource, requires careful management to insure continuing benefits, and (2) the lack of substantial commercial fisheries that would focus attention on and financial investment in the estuary's living resources.

Among the specific factors that contribute to our lack of scientific understanding of the bay's benthic ecology are the following. First, there have been very few in-depth studies of the factors that regulate reproduction, growth, feeding, and mortality. Such studies would, for example, allow us to distinguish between the factors (e.g., physical disturbances, habitat character, biological interactions, food availability, predation) that affect abundances and distributions of benthic species. Such knowledge is necessary if we wish, for example, to distinguish the effects of

pollutant loadings on shellfish growth, reproduction, and survival, or to enhance the productivity of bay shellfish.

The lack of in-depth studies is, in large part, a reflection of institutional priorities. Most governmental agencies that are concerned with the bay and its resources are not established to conduct basic research. They are, rather, resource management or regulatory in nature. The local institutions that strongly support basic research are few, and of these, the two largest (Stanford University and the University of California at Berkeley) have historically not been active in bay studies: with a few exceptions their aquatic scientists have not used San Francisco Bay as a primary study area (Hedgpeth 1979). A direct result is the lack of in-depth doctoral studies that are so important to the advancement of knowledge in any local area. Scientists affiliated with other local academic and research institutions who could address some of the unanswered questions have difficulty finding the necessary financial support for such studies.

Second, there is a lack of long-term, bay-wide monitoring that would provide quantitative evidence that the bay's benthic community is (or is not) changing over time. This is the case because few governmental agencies and academic institutions have been able to maintain consistent, on-going bay programs of any kind. The only two long-term benthic studies are limited to a single region of the bay (California Department of Water Resources 1986) and a single site (Nichols and Thompson 1985a). The first is a required monitoring program conducted by the California Department of Water Resources as part of its permit to divert water from the Sacramento-San Joaquin river system for irrigation. This program has consisted of semiannual benthic sampling at 11 stations in Suisun Bay and Delta between 1975 and 1979, and monthly sampling at 5 stations in the same area since 1980 (see California Department of Water Resources [1986] for the most recent annual data report). The second study is a research investigation of the factors that contribute to short- and long-term change in the benthic community at three stations on one intertidal mudflat in South Bay (Chapter 3; Nichols and Thompson 1985a). The new Aquatic Habitat Institute

(California State Water Resources Control Board 1982; Section 5.3), in its effort to monitor and evaluate the effects of pollutant discharge on San Francisco Bay, has begun bimonthly benthic sampling at eight stations to distinguish among the factors that contribute to long-term change in the communities sampled. The National Oceanic and Atmospheric Administration (NOAA) recently has begun annual bottom sampling in San Francisco Bay as part of its long-term "National Status and Trends Program" (National Oceanic and Atmospheric Administration 1986). Other pollutant effects monitoring programs are evolving (Section 5.3).

Third, no agency or institution has committed sufficient resources to comprehensively address such critical questions as the role of waste contamination in declines of specific species populations, although early studies demonstrate that contaminants in bay fish are at toxic levels (Jung et al. 1984; Benville et al. 1985; R. B. Spies, University of California, pers. comm.), and that some bay clams show signs of physiological stress during periods of high trace-metal availability (Section 5.3.1; Johansson et al. 1986).

Fourth, the results of many of the publicly funded studies of the bay, if distributed at all, appear (generally without outside peer review) in limited-distribution agency or institution reports ("grey literature"). These reports, for the most part, cannot be found in computerized bibliographic data bases. Knowledge of these reports, for people not on agency distribution lists or who are new to the area, is largely obtained by word of mouth. Many of these studies are, moreover, mandated monitoring studies with very limited spatial and temporal coverage, with no obvious objectives other than to collect data, and often with poorly conceived sampling strategies and limited data analysis. Nonetheless, the reports from these studies are often the only source of information about the biology of specific areas of the bay, or about the levels of specific contaminants or their effects on bay organisms. The fact that we have made reference to more than 40 nonserialized "grey literature" publications, and other unpublished reports, in the preparation of this profile is evidence of this problem.

There is no easy way to overcome the institutional obstacles to increasing the scientific base that underlies our knowledge of San Francisco Bay. A greater appreciation of the value of the bay's natural resources and the recognition that these resources require further study, protection, and enhancement are both necessary if these resources are to benefit bay area inhabitants.

7.4 NEEDS FOR RESEARCH AND MANAGEMENT

Given the early successes for shellfish growing in San Francisco Bay and the apparent continuing potential for commercial and recreational shellfishing (Chapter 6), obvious objectives for the development and management of this resource would include both enhancing existing shellfish beds and protecting them from contamination. We need to determine the specific sources and levels of contamination that affect known shellfish beds. This would involve careful studies of the composition and fates of chemical wastes emanating from both point (known effluent discharge sites) and nonpoint (streams and other sources of untreated runoff) sources of contamination to determine what effects these materials have on nearby populations. We also need to designate those areas with the greatest potential for shellfish growing, then enhance these areas by improving the substrate, seeding the beds (as in McAllister and Moore 1982), and improving public access. Shellfish bed enhancement would also include placing tight controls on the waste discharge sites that might affect these beds under a typical range of hydrodynamic conditions.

Protection and enhancement of shellfish beds alone does not benefit the benthos at large. Because the benthos is critical to the estuarine ecosystem as a natural biological control on waste-derived eutrophication and as a direct source of food for most fish (e.g., striped bass, sturgeon, flounder) and large crustacean species (e.g., crab, shrimp) throughout the bay, and for birds in shallow water, we must direct research toward understanding these links more fully.

There is sufficient evidence from San Francisco Bay studies to suggest that bay

populations are being affected by human activities (Nichols et al. 1986). Therefore, delays in implementing the studies necessary to prove or disprove cause and effect only delay further the implementation of meaningful corrective actions. In particular, we require in-depth studies that focus on well-defined problems (e.g., how much and by what mechanisms the contamination of small clams near waste outfalls affects the resident fish or bird species that feed upon them) in which the questions that are asked can be answered through field and laboratory investigations.

Other issues requiring detailed study include (1) the role of the sediment (with its associated microbial community) in determining the levels of water column constituents (e.g., nutrients, waste contaminants); (2) the rates of sediment transport and deposition in various parts of the bay, how these rates are affected by dredging (both removal and disposal), and how these rates affect benthic species distributions and abundances; and (3) the relative importances of river-borne detritus, sediment microbes, microalgae, and meiofauna as food for invertebrate species in various parts of the bay.

REFERENCES

- Aldrich, F.A. 1961. Seasonal variations in the benthic invertebrate fauna of the San Joaquin River Estuary of California, with emphasis on the amphipod Corophium spinicorne Stimpson. *Proc. Acad. Nat. Sci. Phil.* 113:21-28.
- Anderlini, V.C., J.W. Chapman, D.C. Girvin, S.J. McCormick, A.S. Newton, and R.W. Risebrough. 1975. Heavy metal uptake study. U.S. Army Corps of Engineers dredge disposal study, San Francisco Bay and Estuary, Appendix H. San Francisco. 89 pp.
- Aplin, J.A. 1967. Biological survey of San Francisco Bay 1963-1966. *Calif. Dep. Fish Game, Mar. Resour. Oper. Lab. Rep.* 67-4. 131 pp.
- Armor, C., and P.L. Herrgesell. 1985. Distribution and abundance of fishes in the San Francisco Bay Estuary between 1980 and 1982. *Hydrobiologia* 129:211-227.
- Arnal, R.E., P.J. Quintero, T.J. Conomos, and R. Gram. 1980. Trends in the distribution of recent foraminifera in San Francisco Bay. *Cushman Found. Foraminiferal Res. Spec. Publ.* 19:17-39.
- Atwater, B.F. 1979. Ancient processes at the site of southern San Francisco Bay: movement of the crust and changes in sea level. Pages 31-45 in T.J. Conomos, ed. *San Francisco Bay: the urbanized estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco.
- Atwater, B.F., C.W. Hedel, and E.J. Helley. 1977. Late Quaternary depositional history, Holocene sea-level changes, and vertical crustal movement, southern San Francisco Bay, California. *U.S. Geol. Surv. Prof. Pap.* 1014. 15 pp.
- Atwater, B.F., S.G. Conard, J.N. Dowden, C.W. Hedel, R.L. MacDonald, and W. Savage. 1979. History, landforms, and vegetation of the estuary's tidal marshes. Pages 347-385 in T.J. Conomos, ed. *San Francisco Bay: the urbanized estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco.
- Baird, D., P.R. Evans, H. Milne, and M.W. Pienkowski. 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. *Oceanogr. Mar. Biol. Annu. Rev.* 23:573-597.
- Ball, M.D., and J.F. Arthur. 1981. Phytoplankton settling rates - a major factor in determining estuarine dominance. *Estuaries* 4:246.
- Barrett, E.M. 1963. The California oyster industry. *Calif. Dep. Fish Game Fish Bull.* 123:1-103.
- Bay Conservation and Development Commission. 1983. *San Francisco Bay Plan*. San Francisco. 41 pp.
- Bay Conservation and Development Commission. 1986. *Commercial fishing*, Staff Report. San Francisco. 52 pp.
- Bay Conservation and Development Commission and Institute for the Human Environment. 1981. *Bay edges, a four-part guide to public access and recreation along the edges of San Francisco Bay*. San Francisco.
- Bayne, B.L., J. Widdows, M.N. Moore, P. Salkeld, C.M. Worrall, and P. Donkin. 1982. Some ecological consequences of the physiological and biochemical effects of petroleum compounds on marine molluscs. *Philos. Trans. R. Soc. Lond. Biol. Sci. B.* 297:219-239.

- Benville, P.E., Jr., J.A. Whipple, and M.B. Eldridge. 1985. Acute toxicity of seven alicyclic hexanes to striped bass, Morone saxatilis, and bay shrimp, Crangon franciscorum, in seawater. Calif. Fish Game 71:132-140.
- Beukema, J.J., G.C. Cadee, and J.J.M. Jansen. 1977. Variability of growth rate of Macoma balthica (L.) in the Wadden Sea in relation to availability of food. Pages 69-77 in B.R. Keegan, P.O. Ceidigh, and P.J.S. Boaden, eds. Biology of benthic organisms. Pergamon Press, Oxford, England.
- Boesch, D.F. 1977. A new look at the zonation of benthos along the estuarine gradient. Belle W. Baruch Lib. Mar. Sci. 6:245-266.
- Boesch, D.F., M.L. Wass, and R.W. Virnstein. 1976. The dynamics of estuarine benthic communities. Pages 177-196 in M. Wiley, ed. Estuarine processes, Vol. 1. Academic Press, New York.
- Bolton, H.E. 1927. Fray Juan Crespi, missionary explorer on the Pacific coast 1769-1774. University of California Press, Berkeley. 402 pp.
- Bonnot, P. 1932a. Soft shell clam beds in the vicinity of San Francisco Bay. Calif. Fish Game 18:64-66.
- Bonnot, P. 1932b. The California shrimp industry. Calif. Dep. Fish Game Fish Bull. 38:1-20.
- Bonnot, P. 1935. The California oyster industry. Calif. Fish Game 21:65-80.
- Boothe, P. 1967. The food and feeding habits of four species of San Francisco Bay fish. Calif. Dep. Fish Game Mar. Resour. Oper. Ref. 67-13:1-155.
- Bouwman, L.A., K. Romeijn, and W. Admiraal. 1984. On the ecology of meiofauna in an organically polluted estuarine mudflat. Estuarine Coastal Shelf Sci. 19:633-653.
- Brown and Caldwell Engineers. Unpubl. Survey of the water condition in lower San Francisco Bay: Santa Clara County, California (1954). Report prepared for the City of San Jose, Calif. 49 pp.
- California Department of Water Resources. 1986. Sacramento-San Joaquin Delta water quality surveillance program 1985 -- monitoring results pursuant to conditions set forth in Delta Water Rights Decision 1485, Vol. 3. Sacramento, Calif. 288 pp.
- California State Water Resources Control Board. 1982. Aquatic Habitat Program: plan for assessing the effects of pollutants in the San Francisco Bay - Delta Estuary. Water Resources Control Board Publ. 82-7SP. Sacramento, Calif. 49 pp.
- Carlton, J.T. 1979a. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. Thesis. University of California, Davis. 904 pp.
- Carlton, J.T. 1979b. Introduced invertebrates of San Francisco Bay. Pages 427-444 in T.J. Conomos, ed. San Francisco Bay: the urbanized estuary. Pacific Div., American Association for the Advancement of Science, San Francisco.
- Carpelan, L.H. 1957. Hydrobiology of the Alviso salt ponds. Ecology 38:375-390.
- Chan, G.L. 1972. A study of the effects of the San Francisco Bay oil spill on marine life. Part 1. College of Marin, Kentfield, Calif. 78 pp.
- Chan, G.L. 1974. A study of the effects of the San Francisco Bay oil spill on marine life. Part 2. Recruitment. College of Marin, Kentfield, Calif. 42 pp.
- Chapman, P.M., R.N. Dexter, S.F. Cross, and D.G. Mitchell. 1986. A field trial of the sediment quality triad in San Francisco Bay. U.S. Dep. Comm., NOAA, Natl. Ocean Ser. Tech. Memo. NOS OMA 25. 134 pp.
- Christensen, H., and E. Kanneworff. 1985. Sedimenting phytoplankton as major food source for suspension and deposit feeders in the Oresund. Ophelia 24:223-244.

- CH2M-Hill. 1982. Equivalent protection study intensive investigation, final report. Prepared for Chevron, USA. Emeryville, Calif. 245 pp.
- Citizens for a Better Environment. 1983. Toxics in the Bay--an assessment of the discharge of toxic pollutants to San Francisco Bay by municipal and industrial point sources. San Francisco. 116 pp.
- Cloern, J.E. 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.* 9:191-202.
- Cloern, J.E., and F.H. Nichols, eds. 1985. Temporal dynamics of an estuary: San Francisco Bay. Dr. W. Junk, Dordrecht, Netherlands. 237 pp.
- Cloern, J.E., and R.S. Oremland 1983. Chemistry and microbiology of a sewage spill in South San Francisco Bay. *Estuaries* 6:399-406.
- Cloern, J.E., A.E. Alpine, B.E. Cole, R.L.J. Wong, J.F. Arthur, and M.D. Ball. 1983. River discharge controls phytoplankton dynamics in the northern San Francisco Bay Estuary. *Estuarine Coastal Shelf Sci.* 16:415-429.
- Cloern, J.E., B.E. Cole, R.L.J. Wong, and A.E. Alpine. 1985. Temporal dynamics of estuarine phytoplankton: a case study of San Francisco Bay. *Hydrobiologia* 129:153-176.
- Cole, B.E., and J.E. Cloern. 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Mar. Ecol. Prog. Ser.* 17:15-24.
- Conomos, T.J., and D.H. Peterson. 1977. Suspended-particle transport and circulation in San Francisco Bay: an overview. Pages 82-97 in M. Wiley, ed. *Estuarine processes*. Vol. 2: Circulation, sediments and transfer of material in the estuary. Academic Press, New York.
- Conomos, T.J., R.E. Smith, D.H. Peterson, S.W. Hager, and L.E. Schemel. 1979. Processes affecting seasonal distributions of water properties in the San Francisco Bay estuarine system. Pages 115-142 in T.J. Conomos, ed. *San Francisco Bay: the urbanized estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco.
- Conomos, T.J., R.E. Smith, and J.W. Gartner. 1985. Environmental setting of San Francisco Bay. *Hydrobiologia* 129:1-12.
- Cook, S.F. 1946. A reconsideration of shellmounds with respect to population and nutrition. *Am. Antiq.* 12:50-53.
- Coull, B.C. 1973. Estuarine meiofauna: review, trophic relationships and microbial interactions. Pages 499-511 in L.H. Stevenson and R.R. Colwell, eds. *Estuarine microbial ecology*. University of South Carolina Press, Columbia.
- Coull, B.C., and S.S. Bell. 1979. Perspectives of marine meiofaunal ecology. Pages 189-216 in R.J. Livingston, ed. *Ecological processes in coastal and marine systems*. Plenum Press, New York.
- Curtis, L.A., and L.E. Hurd. 1981. Nutrient procurement strategy of a deposit-feeding estuarine neogastropod, Ilyanassa obsoleta. *Estuarine Coastal Shelf Sci.* 13:277-285.
- Dahlstrom, W.A., and P.W. Wild. 1983. A history of Dungeness crab fisheries in California. *Calif. Dep. Fish Game Fish Bull.* 172:7-23.
- Daniels, R.A., and P.B. Moyle. 1983. Life history of splittail (*Cyprinidae: Pogonichthys macrolepidotus*) in the Sacramento-San Joaquin Estuary. *U.S. Natl. Mar. Fish. Serv. Fish. Bull.* 81:647-654.
- de Wilde, P.A.W.J. 1975. Influence of temperature on behavior, energy metabolism, and growth of Macoma balthica (L.). Pages 239-256 in H. Barnes, ed. *Proc. 9th Europ. Mar. Biol. Symp.* Aberdeen University Press, Aberdeen, Scotland.
- Diaz, R.J., and D.F. Boesch. 1977. Impact of fluid mud dredged material on benthic communities of the tidal James River, Virginia. *U.S. Army Eng. Waterw. Exp. Stn. Tech. Rep. D-77-45*. Vicksburg, Miss. 57 pp.

- DiSalvo, L.H. 1978. Environmental effects of dredging and disposal in the San Francisco Bay estuarine system. The Association of Bay Area Governments, Berkeley. 51 pp.
- DiSalvo, L.H., H.E. Guard, N. Hirsch, and J. Ng. 1977. Assessment and significance of sediment associated oil and grease in aquatic environments. U.S. Army Eng. Waterw. Exp. Stn. Dredged Mater. Res. Prog. Tech. Rep. D-77-26. Vicksburg, Miss. 146 pp.
- Fauchald, K., and P.A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.* 17:193-284.
- Federal Water Pollution Control Administration. 1967. Effects of the San Joaquin Master Drain on water quality of the San Francisco Bay and Delta. Central Pacific Basins Comprehensive Water Pollution Control Project, San Francisco. 101 pp.
- Fenchel, T. 1969. The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. *Ophelia* 6:1-182.
- Fenchel, T., and T.H. Blackburn. 1979. Bacteria and mineral cycling. Academic Press, London. 225 pp.
- Fenchel, T., and J.J. Jorgensen. 1977. Detritus food chains of aquatic ecosystems: the role of bacteria. Pages 1-58 in M. Alexander, ed. *Advances in microbial ecology*. Plenum Press, New York.
- Festa, J.F., and D.V. Hansen. 1976. A two-dimensional numerical model of estuarine circulation: the effects of altering depth and river discharge. *Estuarine Coastal Mar. Sci.* 4:309-323.
- Filice, F.P. 1958. Invertebrates from the estuarine portion of San Francisco Bay and some factors influencing their distributions. *Wasmann J. Biol.* 16:159-211.
- Filice, F.P. 1959. The effects of wastes on the distribution of bottom invertebrates in the San Francisco Bay Estuary. *Wasmann J. Biol.* 17:1-17.
- Fisher, J.P. 1916. Clams in San Francisco Bay. *Calif. Fish Game* 2:209-210.
- Foe, C., and A. Knight 1985a. The effect of phytoplankton and suspended sediment on the growth of Corbicula fluminea (Bivalvia). *Hydrobiologia* 127:105-116.
- Foe, C., and A. Knight. 1985b. Further studies evaluating the freshwater asiatic clam, Corbicula fluminea, for monitoring the sublethal impact of point source discharges. Univ. Calif. (Davis) Dep. Land Air Water Resources Water Sci. Eng. Pap. 4518. 74 pp.
- Foe, C., and A. Knight. 1986. Growth of Corbicula fluminea on algal and artificial diets. *Hydrobiologia* 133:155-164.
- Fong, C.C., K.L. Daniels, and W.W.N. Lee. 1982. A method for assessing the potential impacts of discharges of dredged material into San Francisco Bay. Pages 259-269 in W.J. Kockelman, T.J. Conomos, and A.E. Leviton, eds. *San Francisco Bay, use and protection*. American Association for the Advancement of Science, Pacific Div., San Francisco.
- Fredette, T.J. Unpubl. Richmond Harbor Training Wall sea grass transplanting project. Progress Report submitted to U.S. Army Engineer District, San Francisco (1986). U.S. Army Eng. Waterw. Exp. Stn., Vicksburg, Miss. 17 pp.
- Frey, H.W. 1971. California's living marine resources and their utilization. California Department of Fish and Game, Sacramento. 148 pp.
- Fuller, C.C. 1982. The use of Pb-210, Th-234 and Cs-137 as tracers of sedimentary processes in San Francisco Bay, California. M.S. Thesis, University of Southern California, Los Angeles. 251 pp.
- Ganssle, D. 1966. Fishes and decapods of San Pablo and Suisun Bays. *Calif. Dep. Fish Game Fish Bull.* 133:64-94.
- Gerlach, S.A., A.E. Hahn, and M. Schrage. 1985. Size spectra of benthic biomass and metabolism. *Mar. Ecol. Prog. Ser.* 26:161-173.

- Gilbert, G.K. 1917. Hydraulic-mining debris in the Sierra Nevada. U.S. Geol. Surv. Prof. Pap. 105:1-154.
- Goldberg, E.D. 1986. The mussel watch concept. Environ. Monit. Assess. 7:91-103.
- Goldberg, E.D., V.T. Bowen, J.W. Farrington, G. Harvey, J.H. Martin, P.L. Parker, R.W. Risebrough, W. Robertson, E. Schneider, and E. Gable. 1978. The Mussel Watch. Environ. Conserv. 5:101-126.
- Grassle, J.F., and J.P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Mar. Res. 32:253-284.
- Grassle, J.P., and J.F. Grassle. 1976. Sibling species in the marine pollution indicator Capitella (Polychaeta). Science (Wash., D.C.) 192:567-569.
- Hackney, C.T., and G.F. Yelverton. In press. Effects of human activities and sea level rise on wetland ecosystems in the Cape Fear River Estuary, North Carolina, USA. In D. Whigham, R. Good, and J. Kviet, eds. Wetlands: case studies. Dr. W. Junk Publ., Dordrecht, Netherlands.
- Hammond, D.E., C. Fuller, D. Harmon, B. Hartman, M. Korosec, L.G. Miller, R. Rea, S. Warren, W. Berelson, and S.W. Hager. 1985. Benthic fluxes in San Francisco Bay. Hydrobiologia 129:69-90.
- Hargrave, B.T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Board Can. 30:1317-1326.
- Hargrave, B.T., N.J. Prouse, G.A. Phillips, and P.A. Neame. 1983. Primary production and respiration in pelagic and benthic communities at two intertidal sites in the upper Bay of Fundy. Can. J. Fish. Aquat. Sci. 40 (Suppl. 1):229-243.
- Hart, E.W. 1966. Shell deposits of southern San Francisco Bay. Calif. Div. Mines Geol. Miner. Inf. Serv. 19:41-45.
- Hartman, B., and D.E. Hammond. 1985. Gas exchange in San Francisco Bay. Hydrobiologia 129:59-68.
- Hedgpeth, J.W. 1968. Bay and estuary (introduction). Pages 231-233 in E.F. Ricketts, J. Calvin, and J.W. Hedgpeth, eds. Between Pacific tides, 4th ed. Stanford University Press, Stanford, Calif.
- Hedgpeth, J.W. 1979. San Francisco Bay--the unsuspected estuary, a history of researches. Pages 9-29 in T.J. Conomos, ed. San Francisco Bay: the urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco.
- Heip, C. 1980. Meiobenthos as a tool in the assessment of marine environmental quality. Rapp. P.V. Reun. Cons. Int. Explor. Mer 179:182-187.
- Heubach, W., R.J. Toth, and A. McCready. 1963. Food of young-of-the-year striped bass (Roccus saxatilis) in the Sacramento-San Joaquin River system. Calif. Fish Game 49:224-239.
- Hill, C.L., and C.A. Kofoid. 1927. Marine borers and their relation to marine construction on the Pacific coast. San Francisco Bay Marine Piling Commission, San Francisco, Calif. 357 pp.
- Hirsch, N.D., L.H. DiSalvo, and R. Peddicord. 1978. Effects of dredging and disposal on aquatic organisms. U.S. Army Eng. Waterw. Exp. Stn. Dredged Mater. Res. Prog. Tech. Rep. DS-78-5. Vicksburg, Miss. 41 pp.
- Hopkins, D.R. 1986. Atlas of the distributions and abundances of common benthic species in San Francisco Bay, California. U.S. Geol. Surv. Water Resour. Invest. Rep. 86-4003. 16 pp.
- Hopkins, D.R. 1987. Temporal variations in the benthic communities at four intertidal sites in San Francisco Bay, California, 1983-1985. U.S. Geol. Surv. Open File Rep. 87-387. 89 pp.
- Howell, D.G. 1985. Terranes. Sci. Am. 253:116-125.
- Horne, A.J., and A. Nonomura. 1976. Drifting macroalgae in estuarine water: interactions with salt marsh and human communities. Univ. Calif. (Berkeley) Sanit. Eng. Res. Lab. Rep. 76-3. 76 pp.

- Hughes, J.R., W.E. Ames, D.A. Misitano, and G.F. Slusser. 1978. Effects of dredged material disposal on demersal fish and shellfish in Elliott Bay, Seattle, Washington. U.S. Army Eng. Waterw. Exp. Stn. Dredged Mater. Res. Prog. Tech. Rep. D-77-24. Vicksburg, Miss.
- Hummel, H. 1985. Food intake of Macoma balthica (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. *Neth. J. Sea Res.* 19:52-76.
- JBF Scientific Corporation. 1975. Dredging technology study. U.S. Army Corps of Engineers dredge disposal study, San Francisco Bay and estuary, Appendix M. San Francisco. 307 pp.
- Johansson, C., D.J. Cain, and S.N. Luoma. 1986. Variability in the fractionation of Cu, Ag, and Zn among cytosolic proteins in the bivalve Macoma balthica. *Mar. Ecol. Prog. Ser.* 28:87-97.
- Johns, G.E., and R. Bachman. 1982. Aquatic habitat program plan for assessing the effects of pollutants in the San Francisco Bay-Delta Estuary. Calif. State Water Resources Control Board Publ. 82-7SP. 49 pp.
- Jones, L.L. 1940. An introduction of an Atlantic crab into San Francisco Bay. *Proc. 6th Pacific Sci. Congr., Pacific Sci. Assoc.* 3:485-486.
- Jones, M.L. 1961. A quantitative evaluation of the benthic fauna off Point Richmond, California. *Univ. Calif. Publ. Zool.* 67:219-320.
- Jones and Stokes Assoc., Inc. 1977. San Francisco Bay shellfish: an assessment of the potential for commercial and recreational harvesting. Association of Bay Area Governments, Berkeley, Calif. 171 pp.
- Josselyn, M. 1983. The ecology of San Francisco tidal marshes: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-83/23. 102 pp.
- Josselyn, M.N. 1984. Field and bioassay studies on the impact of San Luis Drain water on estuarine macroalgae. In Report of waste discharge estuarine disposal, San Luis Unit, Central Valley Project, California. U.S. Department of the Interior, Bureau of Reclamation, Sacramento. 47 pp.
- Josselyn, M.N., and J.A. West. 1985. The distribution and temporal dynamics of the estuarine macroalgal community of San Francisco Bay. *Hydrobiologia* 129:139-152.
- Jung, M., J.A. Whipple, and M. Moser. 1984. A study of the effects of pollutants on the San Francisco Bay-Delta striped bass fishery. Summary report of the Cooperative Striped Bass Study (COSBS). Institute for Aquatic Resources, Santa Cruz, Calif.
- Kemp, W.M., and W.R. Boynton. 1981. External and internal factors regulating metabolic rates of an estuarine benthic community. *Oecologia (Berl.)* 51:19-27.
- Kinnetic Laboratories, Inc. 1983. Life history analysis of Ampelisca milleri final report--predischarge monitoring program. East Bay Dischargers Authority, San Lorenzo, Calif. 173 pp.
- Klingeman, P.C., and W.J. Kaufman. 1963. Transport of radionuclides with San Francisco Bay sediments, progress report, 1961-62 water year. *Univ. Calif. (Berkeley) Sanit. Eng. Res. Lab. Rep.* 70 pp.
- Klingeman, P.C., and W.J. Kaufman. 1965. Transport of radionuclides with suspended sediment in estuarine systems. *Univ. Calif. (Berkeley) Sanit. Eng. Res. Lab. Rep.* 65-17. 222 pp.
- Knight, A.W., J.W. Sharp, and R.M. Sitts. 1980. Trophic relationships of detritus in the Sacramento-San Joaquin Delta Estuary. *Univ. Calif. (Davis) Water Resour. Cent. Proj. UCAL-WRC-W513.* 185 pp.
- Kremer, J.N., and S.W. Nixon. 1978. A coastal marine ecosystem--simulation and analysis. Springer-Verlag, Berlin. 217 pp.
- Krone, R.B. 1979. Sedimentation in the San Francisco Bay system. Pages 85-96 in T.J. Conomos, ed. *San Francisco Bay: the urbanized estuary.* Pacific Div., American Association for the Advancement of Science, San Francisco.

- Kuenzler, E.J. 1961. Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnol. Oceanogr.* 6:191-204.
- Kuipers, B.R., P.A.W.J. de Wilde, and F. Creutzberg. 1981. Energy flow in a tidal flat ecosystem. *Mar. Ecol. Prog. Ser.* 5:215-221.
- Langlois, G.W. 1980. Aspects of the population biology of the ribbed mussel, Ischadium demissum, in a South San Francisco Bay salt marsh. M.S. Thesis. California State University, Hayward. 95 pp.
- Langton, R.W., J.E. Winter, and O.A. Roels. 1977. The effect of ration size on the growth efficiency of the bivalve mollusc Tapes japonica. *Aquaculture* 12:283-292.
- Laws, R.A. 1983. Quaternary diatom floras and Pleistocene paleogeography of San Francisco Bay. Ph.D. Thesis. University of California, Berkeley. 352 pp.
- Lee, G.F. 1970. Factors affecting the transfer of materials between water and sediments. Univ. Wis. (Madison), Water Resour. Cen., Eutrophication Inf. Program Lit. Rev. 1.
- Liu, D.H.W., K.D. Martin, and C.R. Norwood. 1975. San Francisco Bay benthic community study--technical evaluation. U.S. Army Corps of Engineers dredge disposal study, San Francisco Bay and estuary, Appendix D. San Francisco. 244 pp.
- Long, E.R., and P.M. Chapman. 1985. A sediment quality triad: measures of sediment contamination, toxicity and infaunal community composition in Puget Sound. *Mar. Pollut. Bull.* 16:405-415.
- Lu, J.C.S., and K.Y. Chen. 1977. Migration of trace metals in interfaces of seawater and polluted surficial sediments. *Environ. Sci. Technol.* 11:174-182.
- Luoma, S.N. 1977. Detection of trace contaminant effects in aquatic ecosystems. *J. Fish. Res. Board Can.* 34:436-439.
- Luoma, S.N., and J.E. Cloern. 1982. The impact of waste-water discharge on biological communities in San Francisco Bay. Pages 137-160 in W.J. Kockelman, T.J. Conomos, and A.E. Leviton, eds. *San Francisco Bay: use and protection*. Pacific Div., American Association for the Advancement of Science, San Francisco.
- Luoma, S.N., D.J. Cain, K. Ho, and A. Hutchinson. 1983. Variable tolerance to copper in two species from San Francisco Bay. *Mar. Environ. Res.* 10:209-222.
- Luoma, S.N., D. Cain, and C. Johansson. 1985. Temporal fluctuations of silver, copper and zinc in the bivalve Macoma balthica at five stations in South San Francisco Bay. *Hydrobiologia* 129:109-120.
- Marine Bioassay Laboratories. 1984. Aquatic bioassays for the San Luis Drain central valley project, California, main report, Vol. I. In Report of waste discharge estuarine disposal, San Luis Unit, Central Valley Project, California. U.S. Department of the Interior, Bureau of Reclamation, Sacramento. 205 pp.
- Marshall, N. 1970. Food transfer through the lower trophic levels of the benthic environment. Pages 52-66 in J.H. Steele, ed. *Marine food chains*. Oliver and Boyd, Edinburgh, Scotland.
- Martin, M., G. Ichikawa, J. Goetzl, M. de los Reyes, and M.D. Stephenson. 1984. Relationships between physiological stress and trace toxic substances in the bay mussel, Mytilus edulis, from San Francisco Bay, California. *Mar. Environ. Res.* 11:91-110.
- McAllister, R.D., and T.O. Moore, Jr. 1982. Selected shellfish resources of San Francisco Bay: their distribution, abundance, use, public access, and recommended management alternatives. California Department of Fish and Game and San Francisco Bay Regional Water Quality Control Board, Oakland. 168 pp.
- McCall, P.L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.* 35:221-266.

- McCauley, J.E., R.A. Parr, and D.R. Hancock. 1977. Benthic infauna and maintenance dredging: a case study. *Water Res.* 11:235-242.
- McIntyre, A.D. 1977. Effects of pollution on inshore benthos. Pages 301-318 in B.C. Coull, ed. *Ecology of marine benthos*. University of South Carolina Press, Columbia.
- McKeechie, R.J., and R.B. Fenner. 1971. Food habits of white sturgeon (Acipenser transmontanus) in San Pablo and Suisun Bays, California. *Calif. Fish Game* 57:209-212.
- Meral, G.H. 1982. A history of diversions. Pages 165-169 in W.J. Kockelman, T.J. Conomos, and A.E. Leviton, eds. *San Francisco Bay, use and protection*. Pacific Div., American Association for the Advancement of Science, San Francisco.
- Miller, L.G., R.S. Oremland, and S. Paulsen. 1986. Measurement of nitrous oxide reductase activity in aquatic sediments. *Appl. Environ. Microbiol.* 51:18-24.
- Mills, E.L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. *J. Fish. Res. Board Can.* 24: 305-355.
- Morton, B. 1974. Some aspects of the biology, population dynamics, and functional morphology of Musculista senhousia Benson (Bivalvia, Mytilidae). *Pac. Sci.* 28:19-33.
- Morton, J.W. 1977. Ecological effects of dredging and dredge spoil disposal: a literature review. U.S. Fish Wildl. Serv. Tech. Pap. 94:1-33.
- National Academy of Sciences. 1980. The international mussel watch. Report of a workshop sponsored by the Environmental Studies Board, Commission on Natural Resources, National Research Council. National Academy of Sciences, Washington, D.C. 248 pp.
- National Oceanic and Atmospheric Administration. 1986. The national status and trends program for marine environmental quality, program description. Ocean Assessments Division, NOAA. Washington, D.C. 34 pp.
- Neff, J.W., R.S. Foster, and J.F. Slowey. 1978. Availability of sediment-absorbed heavy metals to benthos with particular emphasis on deposit feeding infauna, final report. U.S. Army Eng. Waterw. Exp. Stn. Dredged Mater. Res. Prog. Tech. Rep D-78-42. Vicksburg, Miss. 286 pp.
- Nelson, N.C. 1909. Shellmounds of the San Francisco Bay region. Univ. Calif. Publ. Am. Archaeol. Ethnol. 7:309-348.
- Nelson, N.C. 1910. The Ellis Landing shellmound. Univ. Calif. Publ. Am. Archaeol. Ethnol. 7:357-426.
- Newell, R.C. 1970. Biology of intertidal animals. American Elsevier Publ. Co., Inc., New York. 555 pp.
- Nichols, F.H. 1973. A review of benthic faunal surveys in San Francisco Bay. U.S. Geol. Surv. Circ. 677. 20 pp.
- Nichols, F.H. 1979. Natural and anthropogenic influences on benthic community structure in San Francisco Bay. Pages 409-426 in T.J. Conomos, ed. *San Francisco Bay: the urbanized estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco.
- Nichols, F.H. 1985a. Abundance fluctuations among benthic invertebrates in two Pacific estuaries. *Estuaries* 8:136-144.
- Nichols, F.H. 1985b. Increased benthic grazing: an alternative explanation for low phytoplankton biomass in northern San Francisco Bay. *Estuarine Coastal Shelf Sci.* 21:379-388.
- Nichols, F.H., J.E. Cloern, S.N. Luoma, and D.H. Peterson. 1986. The modification of an estuary. *Science* (Wash., D.C.) 231:567-573.
- Nichols, F.H., and J.K. Thompson. 1982. Seasonal growth in the bivalve Macoma balthica near the southern limit of its range. *Estuaries* 5:110-120.
- Nichols, F.H., and J.K. Thompson. 1985a. Persistence of an introduced mudflat community in South San Francisco Bay, California. *Mar. Ecol. Prog. Ser.* 24:83-97.

- Nichols, F.H., and J.K. Thompson. 1985b. Time scales of change in the San Francisco Bay benthos. *Hydrobiologia* 129:121-138.
- Nixon, S.W. 1981. Remineralization and nutrient cycling in coastal marine ecosystems. Pages 111-138 in B.J. Neilson and L.E. Cronin, eds. *Estuaries and nutrients*. The Humana Press, Clifton, N.J.
- Officer, C.B., R.B. Biggs, J.L. Taft, L.E. Cronin, M.A. Tyler, and W.R. Boynton. 1984. Chesapeake Bay anoxia: origin, development, and significance. *Science* (Wash. D.C.) 223:22-27.
- Oliver, J.S., P.N. Slaterry, L.W. Hulberg, and J.W. Nybakken. 1977. Patterns of succession in benthic infaunal communities following dredging and dredged material disposal in Monterey Bay. U.S. Army Eng. Waterw. Exp. St. Dredged Mater. Res. Prog. Environ. Effects Lab. Tech. Rep. D-77-27. Vicksburg, Miss. 186 pp.
- O'Neal, G., and J. Sceva. 1971. The effects of dredging on water quality in the Northwest. Environmental Protection Agency, Office of Water Programs, Region 10, Seattle. 158 pp.
- Oremland, R.S. 1979. Methanogenic activity in plankton samples and fish intestines: a mechanism for in situ methanogenesis in oceanic surface waters. *Limnol. Oceanogr.* 24:1136-1141.
- Oremland, R.S. 1981. Microbial formation of ethane in anoxic estuarine sediments. *Appl. Environ. Microbiol.* 42:122-129.
- Oremland, R.S., and S. Polcin. 1982. Methanogenesis and sulfate reduction: Competitive and noncompetitive substrates in estuarine sediments. *Appl. Environ. Microbiol.* 44:1270-1276.
- Oremland, R.S., and M. P. Silverman. 1979. Microbial sulfate reduction measured by an automated electrical impedance technique. *Geomicrobiol. J.* 1:355-372.
- Oremland, R.S., L.M. Marsh, and S. Polcin. 1982. Methane production and simultaneous sulphate reduction in anoxic, salt marsh sediments. *Nature* (Lond.) 296:143-145.
- Oremland, R.S., C. Umberger, C.W. Culbertson, and R.L. Smith. 1984. Denitrification in San Francisco Bay intertidal sediments. *Appl. Environ. Microbiol.* 47:1106-1112.
- Painter, R.E. 1966. Zoobenthos of San Pablo and Suisun Bays. Calif. Dep. Fish Game Fish Bull. 133:40-56.
- Pamatmat, M.M. 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. *Int. Rev. Gesamten. Hydrobiol.* 53:211-298.
- Pamatmat, M.M. 1977. Benthic community metabolism: a review and assessment of present status and outlook. Pages 89-111 in B.C. Coull, ed. *Ecology of marine benthos*. University of South Carolina Press, Columbia.
- Pamatmat, M.M. 1984. Measuring the metabolism of the benthic ecosystem. Pages 223-246 in M.J.R. Fasham, ed. *Flows of energy and materials in marine ecosystems. Theory and practice*. Plenum Press, New York.
- Pamatmat, M.M. 1986. Problems with empirical models of sediment oxygen demand. Pages 23-36 in K.J. Hatcher, ed. *Sediment oxygen demand -- processes, modeling and measurement*. Institute of Natural Resources, University of Georgia, Athens, Georgia.
- Pamatmat, M.M., R.S. Jones, H. Sanborn, and A. Bhagwat. 1973. Oxidation of organic matter in sediments. EPA-660/3-73-005. U.S. Gov. Print. Off, Wash., DC. 104 pp.
- Parsons, T.R., M. Takahashi, and B. Hargrave. 1984. *Biological oceanographic processes*, 3rd ed. Pergamon Press, Oxford, England. 330 pp.
- Pearson, E.A. 1958. "Reduced area" investigation of San Francisco Bay. California State Water Pollution Control Board, Sacramento. 328 pp.
- Peddicord, R.K., V.A. McFarland, D.P. Belfiori, and T.E. Byrd. 1975. Effects of suspended solids on San Francisco Bay organisms. U.S. Army Corps of Engineers Dredge Disposal Study, San Francisco Bay and estuary, Appendix G. San Francisco. 158 pp.

- Peterson, C.H., and N.M. Peterson. 1979. The ecology of intertidal flats of North Carolina: a community profile. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-79/39. 73 pp.
- Peterson, D.H., R.E. Smith, S.W. Hager, D.D. Harmon, R.E. Herndon, and L.E. Schemel. 1985. Interannual variability in dissolved inorganic nutrients in northern San Francisco Bay Estuary. *Hydrobiologia* 129:37-58.
- Phillips, R.C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-84/24. 85 pp.
- Porterfield, G., N.L. Hawley, and C.A. Dunnam. 1961. Fluvial sediments transported by streams tributary to the San Francisco Bay area. U.S. Geol. Surv. Open File Rep. 70 pp.
- Race, M.S. 1981. Field ecology and natural history of Cerithidea californica (Gastropoda: Prosobranchia) in San Francisco Bay. *Veliger* 24:18-27.
- Race, M.S. 1982. Competitive displacement and predation between introduced and native mud snails. *Oecologia* (Berl.) 54:337-347.
- Radtke, L.D. 1966. Distribution of smelt, juvenile sturgeon and starry flounder in the Sacramento-San Joaquin Delta with observations on food of sturgeon. Calif. Dep. Fish Game Fish Bull. 136:115-129.
- Recher, H.F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47:393-407.
- Reise, K. 1979. Moderate predation on meiofauna by the macrobenthos of the Wadden Sea. *Helgol. Wiss. Meeresunters.* 32:453-465.
- Risebrough, R.W., J.W. Chapman, R.K. Okazaki, and T.T. Schmidt. 1977. Toxicants in San Francisco Bay and estuary. Association of Bay Area Governments, Berkeley. 80 pp.
- Rosenfield, A. 1976. Infectious diseases in commercial shellfish on the middle Atlantic coast. Pages 414-423 in M.G. Gross, ed. Middle Atlantic Continental Shelf and the New York Bight. Am. Soc. Limnol. Oceanogr. Spec. Symp. 2.
- Rotramel, G. 1972. Iais californica and Sphaeroma quoyanum, two symbiotic isopods introduced to California (Isopoda, Janiridae and Sphaeromatidae). *Crustaceana*, Suppl. 3:193-197.
- Rozengurt, M.A., and M.J. Herz. 1981. Water, water everywhere but just so much to drink. *Oceans Mag.* 14:65-67.
- Rubin, D.M., and D.S. McCulloch. 1979. The movement and equilibrium of bedforms in central San Francisco Bay. Pages 97-113 in T.J. Conomos, Ed., San Francisco Bay: the urbanized estuary. Pacific Div., American Association for the Advancement of Science, San Francisco.
- Russell, P.P., T.A. Bursztynsky, L.A. Jackson, and E.Y. Leong. 1982. Water and waste inputs to San Francisco Estuary - an historical perspective. Pages 127-136 in W.J. Kockelman, T.J. Conomos, and A.E. Leviton, eds. San Francisco Bay, use and protection. American Association for the Advancement of Science, Pacific Div., San Francisco.
- Russo, R.A. 1975. Observations of the food habits of leopard sharks (Triakis semifasciata) and brown smoothhounds (Mustelus henlei). *Calif. Fish Game* 61:95-103.
- Sawyer, C.N. 1965. The sea lettuce problem in Boston Harbor. *J. Water Pollut. Control Fed.* 37:1122-1133.
- Schneider, M.R. 1976. Population dynamics of the symbiotic marine isopods, Sphaeroma quoyana and Iais californica. M.S. Thesis. California State University, San Francisco. 85 pp.
- Sellmer, G.P. 1967. Functional morphology and ecological life history of the gem clam, Gemma gemma (Eulamellibranchia: Veneridae). *Malacologia* 5:137-223.
- Setchell, W.A. 1929. Morphological and phenological notes on Zostera marina (L.). *Univ. Calif. Publ. Bot.* 14:389-452.
- Shellem, B.H., and M.N. Josselyn. 1982. Physiological ecology of Enteromorpha clathrata (Roth) Greville on a salt marsh mudflat. *Bot. Mar.* 25:541-549.

- Shuba, P.J., H.E. Tatem, and J.H. Carroll. 1978. Biological assessment methods to predict the impact of open-water disposal of dredged material. U.S. Army Eng. Waterw. Exp. Stn. Dredged Mater. Res. Prog. Tech. Rep. D-78-50. Vicksburg, Miss. 162 pp.
- Siegfried, C.A., M.E. Kopache, and A.W. Knight. 1980. The benthos of a portion of the Sacramento (San Francisco Bay Estuary) during a dry year. *Estuaries* 3:296-307.
- Silva, P.C. 1979. The benthic algal flora of central San Francisco Bay. Pages 287-345 in T.J. Conomos, ed. San Francisco Bay: the urbanized estuary. Pacific Div., American Association for the Advancement of Science, San Francisco.
- Skinner, J.E. 1962. An historical review of the fish and wildlife resources of the San Francisco Bay area. Calif. Dep. Fish Game Resour. Agency Water Projects Branch Rep. 1:1-226.
- Smith, K.L., Jr. G.T. Rowe, and J.A. Nichols. 1974. Benthic community respiration near the Woods Hole sewage outfall. *Estuarine Coastal Mar. Sci.* 1:65-70.
- Smith, R.L., and R.S. Oremland. 1983. Anaerobic oxalate degradation: widespread natural occurrence in aquatic sediments. *Appl. Environ. Microbiol.* 46:106-113.
- Smith, S.E., and S. Kato. 1979. The fisheries of San Francisco Bay: past, present and future. Pages 445-468 in T.J. Conomos, ed. San Francisco Bay, the urbanized estuary. Pacific Div., American Association for the Advancement of Science, San Francisco.
- Soulsby, P.G., D. Lowthion, and M. Houston. 1978. Observations on the effects of sewage discharged into a tidal harbour. *Mar. Pollut. Bull.* 9:242-245.
- Stein, J.E., and J.G. Denison. 1966. In situ benthic oxygen demand of cellulosic fibers. *Advances in Water Pollution Research. Proc. Third Int. Conf. Water Pollut. Control Fed.* 3:181-190.
- Stenstrom, M.K., G.S. Silverman, and T.A. Bursztynsky. 1984. Oil and grease in urban stormwater. *Am. Soc. Civil Eng. J. Environ. Eng. Div.* 110:58-72.
- Stephenson, M.D., M. Martin, S.E. Lange, A.R. Flegal, and J.H. Martin. 1979. California mussel watch 1977-1978, Vol. 2, trace metal concentrations in the California mussel *Mytilus californianus*. California State Water Resources Control Board, Water Qual. Monit. Rep. 79-22. Sacramento. 110 pp.
- Stevens, D.E. 1966. Distribution and food habits of the American shad (*Alosa sapidissima*) in the Sacramento-San Joaquin Delta. Calif. Dep. Fish Game Fish Bull. 136:97-107.
- Storrs, P.N., R.E. Selleck, and E.A. Pearson. 1965. A comprehensive study of San Francisco Bay 1963-64. Univ. Calif. (Berkeley) Sanit. Eng. Res. Lab. Rep. 65-1. 181 pp.
- Storrs, P.N., E.A. Pearson, and R.E. Selleck. 1966. A comprehensive study of San Francisco Bay, final report. V. Summary of physical, chemical, and biological water and sediment data. Univ. Calif. (Berkeley) Sanit. Eng. Res. Lab. Rep. 67(2):1-140.
- Sustar, J.F. 1982. Sediment circulation in San Francisco Bay. Pages 271-279 in W.J. Kockelman, T.J. Conomos, and A.E. Leviton, eds. San Francisco Bay, use and protection. Pacific Div., American Association for the Advancement of Science, San Francisco.
- Sutton, J.E. 1978. Survey of sport shellfishing potential in San Francisco Bay, in southern San Francisco and northern San Mateo Counties, Final Report. City and County of San Francisco Wastewater Program. 77 pp.
- Sutton, J.E., and Jefferson Associates, Inc. 1981. Shellfish resources of eastern San Francisco Bay: distribution, abundance, public access and use. Special District No. 1., East Bay Municipal Utility District, Oakland, Calif. 169 pp.
- Teal, J.M., and J. Kanwisher. 1961. Gas exchange in a Georgia salt marsh. *Limnol. Oceanogr.* 6:388-399.

- Thayer, G.W., W.J. Kenworthy, and M.S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic Coast: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-84/02. 147 pp.
- Thomas, J.L. 1967. The diet of juvenile and adult striped bass (Roccus saxatilis) in the Sacramento-San Joaquin River system. Calif. Fish Game 53:49-62.
- Thomas, J.P., W.C. Phoel, F.W. Steimle, J.E. O'Reilly, and C.A. Evans. 1976. Seabed oxygen consumption - New York Bight apex. Pages 354-369 in M.G. Gross, ed. Middle Atlantic Continental Shelf and the New York Bight. Am. Soc. Limnol. Oceanogr. Spec. Symp. 2.
- Thompson, J.K. 1982. Population structure of Gemma gemma in South San Francisco Bay, with a comparison to some Northeastern United States estuarine populations. Veliger 24:281-290.
- Thompson, J.K., and F.H. Nichols 1981. Benthic macrofaunal biomass of San Francisco Bay, California: January/February and August 1973. U.S. Geol. Surv. Open File Rep. 81-1331. 39 pp.
- Thompson, J.K., and F.H. Nichols. In Press. Food availability controls the seasonal cycle of growth in the bivalve Macoma balthica in San Francisco Bay, California. J. Exp. Mar. Biol. Ecol.
- Thompson, J.K., F.H. Nichols, and S.M. Wienke 1981. Distribution of benthic chlorophyll in San Francisco Bay, California, February 1980 - February 1981. U.S. Geol. Surv. Open File Rep. 81-1134. 36 pp.
- Thomson, E.A., S.N. Luoma, C.E. Johansson, and D.J. Cain. 1984. Comparison of sediments and organisms in identifying sources of biologically available trace metal contamination. Water Res. 18:755-765.
- Thomson-Becker, E.A., and S.N. Luoma. 1985. Temporal fluctuations in grain size, organic materials and iron concentrations in intertidal surface sediment of San Francisco Bay. Hydrobiologia 129:91-107.
- U.S. Army Corps of Engineers. 1976. Water column. U.S. Army Corps of Engineers dredge disposal study, San Francisco Bay and estuary, Appendix C. San Francisco. 98 pp.
- U.S. Army Corps of Engineers. 1977. Main report. U.S. Army Corps of Engineers dredge disposal study, San Francisco Bay and estuary. San Francisco. 113 pp.
- U.S. Fish and Wildlife Service, and California Department of Fish and Game. 1979. Protection and restoration of San Francisco Bay fish and wildlife habitat. Report prepared by Jones and Stokes, Assoc., Inc., Harvey and Stanley Assoc, Inc., and John Blayne Assoc. 2 vols.
- van der Burgh, I. P. 1968. Prediction of the extent of saltwater intrusion into estuaries and seas. J. Hydraul. Res. 6:267-288.
- Vogel, T.M., R.S. Oremland, and K.A. Kvenvolden 1982. Low-temperature formation of hydrocarbon gases in San Francisco Bay sediment (California, U.S.A.). Chem. Geol. 37:289-298.
- Wahle, R.A. 1985. The feeding ecology of Crangon franciscorum and Crangon nigricauda in San Francisco Bay, California. J. Crustacean Biol. 5:311-326.
- Walters, R.A., R.T. Cheng, and T.J. Conomos. 1985. Time scales of circulation and mixing processes of San Francisco Bay waters. Hydrobiologia 129:13-36.
- Warren, C.E., and G.E. Davis. 1967. Laboratory studies on the feeding, bioenergetics and growth of fish. Pages 175-214 in S.D. Gerking, ed. The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, England.
- Wild, P.W., and R.N. Tasto, eds. 1983. Life history, environment, and mariculture studies of the Dungeness crab, Cancer magister, with emphasis on the central California fishery resource. Calif. Dep. Fish Game Fish Bull. 172:1-352.
- Wilkinson, L. 1963. Nitrogen transformation in a polluted estuary. Int. J. Water Pollut. 7:737-752.

Wolff, W. J. 1977. A benthic food budget for the Grevelingen Estuary, The Netherlands, and a consideration of the mechanisms causing high benthic secondary production in estuaries. Pages 267-280 in B.C. Coull, ed. Ecology of marine benthos. University of South Carolina Press, Columbia.

Wooster, T.W. 1968a. Clams, native oysters and mussels. Pages 123-145 in Fish and wildlife resources of San Francisco Bay and Delta: description, environmental requirements, problems, opportunities and the future. Task 7-1B. San Francisco Bay--Delta Water Quality

Control Program. California Department of Fish and Game, Resources Agency, Sacramento.

Wooster, T.W. 1968b. Existing and potential recreational and commercial shellfish production and use in the San Francisco, San Leandro, Richardson, San Rafael and San Pablo Bays complex. California Department of Fish and Game Rep. 89 pp.

Zeitzschel, B. 1980. Sediment-water interactions in nutrient dynamics. Pages 195-218 in K.R. Tenore and B.C. Coull, eds. Marine benthic dynamics. University of South Carolina Press, Columbia.

50272-101

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|--|--------------------|--|--|---|--|--|--|-----------------------|--|---------|-----------|-----------|-----------|-------------|-----------|--|--|----------------------------|--------------------|-----------------|-------------------|--------------------|--|------------------------------|--|
| REPORT DOCUMENTATION PAGE | | 1. REPORT NO. Biological Report 85(7.19) | | 2. | | 3. Recipient's Accession No. | | | | | | | | | | | | | | | | | | | |
| 4. Title and Subtitle The Ecology of the Soft-Bottom Benthos of San Francisco Bay: A Community Profile | | | | | | 5. Report Date September 1988 | | | | | | | | | | | | | | | | | | | |
| | | | | | | 6. | | | | | | | | | | | | | | | | | | | |
| 7. Author(s) Frederic H. Nichols and Mario M. Pamatmat | | | | | | 8. Performing Organization Rept. No. | | | | | | | | | | | | | | | | | | | |
| 9. Performing Organization Name and Address U.S. Geological Survey Tiburon Center for Environmental Studies 345 Middlefield Road San Francisco State University Menlo Park, CA 94025 P.O. Box 855 Tiburon, CA 94920 | | | | | | 10. Project/Task/Work Unit No. | | | | | | | | | | | | | | | | | | | |
| | | | | | | 11. Contract(C) or Grant(G) No. (C) (G) | | | | | | | | | | | | | | | | | | | |
| 12. Sponsoring Organization Name and Address U.S. Department of the Interior Fish and Wildlife Service National Wetlands Research Center Washington, D.C. 20240 | | | | | | 13. Type of Report & Period Covered | | | | | | | | | | | | | | | | | | | |
| | | | | | | 14. | | | | | | | | | | | | | | | | | | | |
| 15. Supplementary Notes | | | | | | | | | | | | | | | | | | | | | | | | | |
| 16. Abstract (Limit: 200 words) <p>Benthic species composition in San Francisco Bay reflects the highly variable environment and the predominance of introduced species. Species abundances vary greatly with season, reflecting both intrinsic (reproduction/mortality) and extrinsic (salinity, sedimentation, wind) factors. Larger year-to-year variations appear associated with climatic patterns and unusual climatic events.</p> <p>Filter feeders predominate, with growth in some species linked to the availability of microalgae. They may prevent the growth of nuisance algal blooms. Benthic invertebrates are, in turn, food for fish, aquatic birds, and humans.</p> <p>Sediments and organisms are contaminated with wastes, but effects at the population level (declines in abundance) or community level (changes in species composition) are not easily distinguished from natural variability. Permanent effects of freshwater diversion or dredging on benthic community structure have not been detected.</p> <p>Shellfish harvesting, once commercially prominent, is restricted to sports digging of two introduced clam species. The renewal of commercial oyster growing, now being considered, requires resolution of contamination issues.</p> <p>The future management of the estuary's benthic resources depends on increased awareness of the need to protect and enhance these resources, on increased commitments to estuarine research, and on improved strategies for overcoming human-induced problems.</p> | | | | | | | | | | | | | | | | | | | | | | | | | |
| 17. Document Analysis <table border="0"> <tr> <td colspan="2">a. Descriptors</td> </tr> <tr> <td>benthos</td> <td>pollution</td> </tr> <tr> <td>estuaries</td> <td>sediments</td> </tr> <tr> <td>food chains</td> <td>shellfish</td> </tr> <tr> <td colspan="2">b. Identifiers/Open-Ended Terms</td> </tr> <tr> <td>benthic community dynamics</td> <td>introduced species</td> </tr> <tr> <td>estuarine fauna</td> <td>San Francisco Bay</td> </tr> <tr> <td>estuary management</td> <td></td> </tr> <tr> <td colspan="2">c. COSATI Field/Group</td> </tr> </table> | | | | | | | | a. Descriptors | | benthos | pollution | estuaries | sediments | food chains | shellfish | b. Identifiers/Open-Ended Terms | | benthic community dynamics | introduced species | estuarine fauna | San Francisco Bay | estuary management | | c. COSATI Field/Group | |
| a. Descriptors | | | | | | | | | | | | | | | | | | | | | | | | | |
| benthos | pollution | | | | | | | | | | | | | | | | | | | | | | | | |
| estuaries | sediments | | | | | | | | | | | | | | | | | | | | | | | | |
| food chains | shellfish | | | | | | | | | | | | | | | | | | | | | | | | |
| b. Identifiers/Open-Ended Terms | | | | | | | | | | | | | | | | | | | | | | | | | |
| benthic community dynamics | introduced species | | | | | | | | | | | | | | | | | | | | | | | | |
| estuarine fauna | San Francisco Bay | | | | | | | | | | | | | | | | | | | | | | | | |
| estuary management | | | | | | | | | | | | | | | | | | | | | | | | | |
| c. COSATI Field/Group | | | | | | | | | | | | | | | | | | | | | | | | | |
| 18. Availability Statement Unlimited | | | | 19. Security Class (This Report) Unclassified | | 21. No. of Pages xi + 73 | | | | | | | | | | | | | | | | | | | |
| | | | | 20. Security Class (This Page) Unclassified | | 22. Price | | | | | | | | | | | | | | | | | | | |

(See ANSI-Z39.18)

 OPTIONAL FORM 272 (4-77)
 (Formerly NTIS-35)
 Department of Commerce